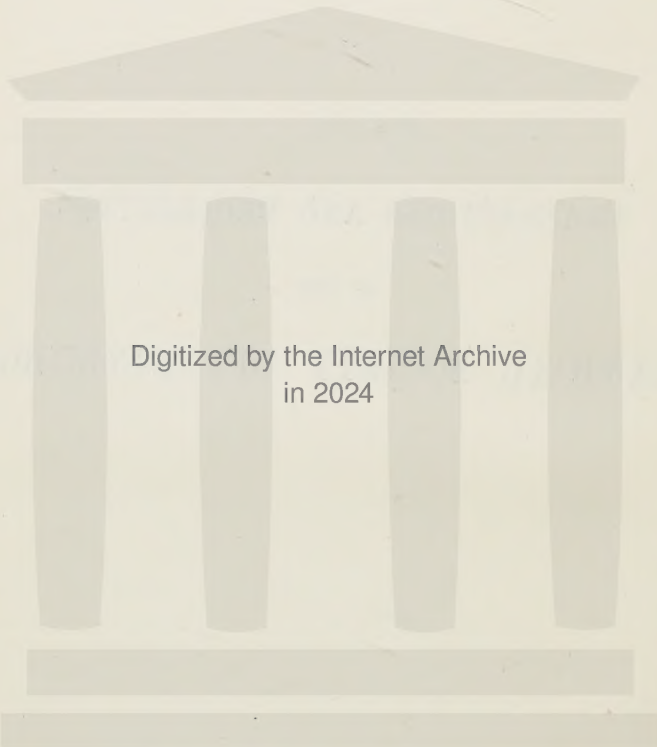


Vol. 34

TRANSACTIONS AND PROCEEDINGS

OF THE

BOTANICAL SOCIETY OF EDINBURGH.



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TRANSACTIONS AND PROCEEDINGS

OF THE

BOTANICAL SOCIETY OF EDINBURGH.

VOLUME XXXIV.

INCLUDING SESSIONS CVIII-CXI.

(1943-1947.)

WITH 10 PLATES AND OTHER ILLUSTRATIONS.



EDINBURGH:

PRINTED FOR THE BOTANICAL SOCIETY.

1948.

Printed in Great Britain by
NEILL & Co., LTD., EDINBURGH.

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PROCEEDINGS
OF THE
BOTANICAL SOCIETY OF EDINBURGH

SESSION CVIII.

OCTOBER 21, 1943.

Dr. MALCOLM WILSON, Vice-President, in the Chair.

The following Office-Bearers were elected for Session 1943-44.

PRESIDENT.

[Not elected.]

VICE-PRESIDENTS.

DAVID CLOUSTON, C.I.E., M.A., D.Sc.	JOHN GARRIOCK, M.A., B.Sc.
E. WYLLIE FENTON, M.A., D.Sc.	WM. McRAE, C.I.E., M.A., D.Sc.

COUNCILLORS.

JOHN ANTHONY, M.C., M.A., B.Sc.	JAMES W. GREGOR, D.Sc.
J. J. BLACKIE, Ph.C., Ph.D.	Prof. J. R. MATTHEWS, M.A.
ALEXANDER COWAN, M.A.	DAVID RUSSELL, LL.D.
JOHN DAVIDSON, B.Sc.(Econ.).	Prof. JOHN WALTON, M.A., D.Sc.
W. EDGAR EVANS, B.Sc.	MALCOLM WILSON, D.Sc.
C. E. FOISTER, B.A., Ph.D.	

Honorary Secretary—H. R. FLETCHER, D.Sc.

Foreign Secretary—Professor Sir WM. WRIGHT SMITH, M.A.

Cryptogamic Secretary—C. E. FOISTER, B.A., Ph.D.

Treasurer—J. W. H. JOHNSON, C.A.

Assistant Secretary—J. T. JOHNSTONE, M.A., B.Sc.

Artist—R. M. ADAM, F.L.S.

Auditor—JOHN DAVIDSON, B.Sc.(Econ.).

The TREASURER, Mr. J. W. H. JOHNSON, C.A., submitted the following Statement of Accounts for Session 1942-43:—

INCOME.	
Annual Subscriptions for 1942-1943	£33 15 0
Do. Arrears	7 15 0
Transactions sold	17 5 0
Interest on Funds Invested and in Bank	13 16 11
Subscriptions to Publications Fund	68 17 3
Income from Botanical Society Trust Fund	11 0 5
Income Tax recovered	14 15 0
	<u>£167 4 7</u>

EXPENDITURE.	
Printing <i>Transactions</i> for Session 1941-1942	£151 12 5
Printing and Postage of Notices for Meetings	21 1 0
Expenses of Lectures	2 6 0
Stationery, Postages, etc.	3 1 3
Fire Insurance on Books	0 5 0
Honorarium to Treasurer	3 3 0
	<u>£181 8 8</u>
Excess of Expenditure	<u>£14 4 1</u>

STATE OF FUNDS.

Life Members' Fund.

Balance of Fund at close of Session 1941-1942	£478 10 7
Add—Life Composition received	10 10 0
Balance as at close of Session	<u>£489 0 7</u>

Ordinary Fund.

Balance of Fund at close of Session 1941-1942	£263 6 5
Less—Decrease during Session 1942-1943	14 4 1
Balance as at close of Session, subject to expense of printing <i>Transactions</i>	<u>249 2 4</u>
Total Funds	<u>£738 2 11</u>

Being:—£200 3½% War Stock, at cost	£194 18 3
£250 London & North Eastern Railway Co. 3% Debenture Stock at cost	216 18 6
£100 3% Defence Bonds	100 0 0
Sums on Deposit Receipt with Union Bank of Scotland, Ltd.	200 0 0
Sum in Current Account with do.	28 6 2

	<u>£740 2 11</u>
Less—Subscriptions received in advance	2 0 0
As above	<u>£738 2 11</u>

Note.—Subscriptions in arrear, considered recoverable, 1941-1942, £5.

1942-1943, £25.

EDINBURGH, 29th September 1943.—I hereby certify that I have audited the Accounts of the Treasurer of the Botanical Society of Edinburgh for Session 1942-1943, and have found them correct. I have also checked the foregoing Abstract, and find it correct. I have seen the securities for the invested funds and have found them in order.

JOHN DAVIDSON, *Auditor.*

BOTANICAL SOCIETY TRUST FUND.

SESSION 1942-1943.

INCOME.

Interest on Funds invested	£11 0 5
--------------------------------------	---------

EXPENDITURE.

To Publications Fund	£11 0 5
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EDINBURGH, 1st October 1943.—I certify that I have examined the above account and relative vouchers of the Edinburgh Botanical Society Trust Fund, and found the same to be correct.

ALEX. ARNOTT.

Professor LILY NEWTON, Mr. JAS. MCARTHUR TODD, and Miss EMILY A. K. FERGUSON were elected Ordinary Fellows.

Miss M. M. CATTANACH was elected a Lady Member.

Miss M. S. KIMPTON, Miss C. G. T. SCOTT, Mr. H. H. DAVIDIAN, Mr. S. F. HAYES, and Mr. N. F. ROBERTSON were elected Ordinary Members.

The CHAIRMAN announced the death of Professor JOHN M. MACFARLANE, Emeritus Professor of Botany of the University of Pennsylvania, at the age of 87. He had been a Fellow since 1881.

The CHAIRMAN also intimated the death of Dr. FRED STOKER, who had been a fellow since 1936.

The death of an Hon. Foreign Fellow, Dr. HEINRICH HANDEL-MAZZETTI, as a result of a motor accident in 1940, was also announced.

Mr. DAVID WILKIE read a paper on Plants of Recent Introduction, which he illustrated with a large number of lantern slides.

NOVEMBER 11, 1943.

Dr. E. WYLLIE FENTON, Vice-President, in the Chair.

ELECTION OF PRESIDENT—Dr. E. WYLLIE FENTON was unanimously elected President for Session 1943-44.

Mr. M. Y. ORR read a paper on the Leaf Anatomy of *Podocarpus* (see p. 1).

A number of plants in flower were shown from the Royal Botanic Garden, including *Gaultheria Wardii* Marq. et Shaw, *Primula blattariformis* Franch., *Stenocarpus sinuatus* Endl., and *Streptocarpus montanus* Oliver.

DECEMBER 16, 1943.

Dr. E. WYLLIE FENTON, President, in the Chair.

Miss M. C. D. MUNRO was elected an Ordinary Fellow.

Dr. MALCOLM WILSON read a paper on the Distribution and Phylogeny of the Rust Fungi, which he illustrated with a number of lantern slides.

A number of plants in flower were shown from the Royal Botanic Garden, also 2 seedlings of *Lilium aurantiacum* growing from the same seed.

JANUARY 20, 1944.

Dr. E. WYLLIE FENTON, President, in the Chair.

Dr. DOROTHY G. DOWNIE read a paper giving a survey of recent work on Orchid Mycorrhiza. She illustrated the paper with a number of lantern slides.

FEBRUARY 24, 1944.

Dr. E. WYLLIE FENTON, President, in the Chair.

Dr. WILLIAM BLACK, Dr. H. C. CHOUDHURI, Dr. ELIZABETH GRAY, and Dr. MARY NOBLE were elected Ordinary Fellows.

The following Motion on Alteration of Laws, moved by Dr. MALCOLM WILSON and seconded by Mr. W. E. EVANS, was unanimously agreed to:—

Chapter V. Office-Bearers.

That paragraph 6 be altered to read:—

The Society shall publish Transactions and Proceedings. The consideration of the acceptance, reading, and publication of all papers is vested in the Council, whose decision shall be final. For the consideration of each paper the Council shall appoint Two Referees who shall submit their reports to the Council through the Honorary Secretary. Acceptance for reading shall not necessarily imply acceptance for publication.

The PRESIDENT announced the death of Sir JOHN BRETLAND FARMER, an Honorary Fellow of the Society since 1907; and also the death of ALEXANDER COWAN, a former President (see p. 211).

Professor WALTON gave an Address on the Vegetation of Spitzbergen, which he illustrated with lantern slides.

MARCH 16, 1944.

Dr. E. WYLLIE FENTON, President, in the Chair.

Mrs. W. J. WALKER TODD and Mr. J. ROBERTS were elected Ordinary Fellows.

Dr. J. W. GREGOR read a paper on Ecotypes and Subspecies, which he illustrated with a number of diagrams.

APRIL 20, 1944.

Dr. E. WYLLIE FENTON, President, in the Chair.

Mrs. C. CAMERON, Mr. FRANK F. BEATTIE, and Mr. WM. T. COWAN were elected Ordinary Members.

Mrs. ANTHONY and Miss STEPHEN were elected Lady Members.

Dr. ERIC V. WATSON read a paper on Glimpses of Vegetation of the U.S.A., which he illustrated with a large number of lantern slides in colour.

MAY 18, 1944.

Dr. E. WYLLIE FENTON, President, in the Chair.

The PRESIDENT announced the death of Sir DAVID PRAIN on the 16th March. He had been a Fellow of the Society since June 1891.

Dr. WILLIAM McRAE read a paper on Sugar Cane in India, which he illustrated with lantern slides. There followed a discussion on the paper, the principal speakers being Dr. WM. BURNS and Dr. DAVID CLOUSTON.

A paper by Dr. BARNETT, "Keys to the Species Groups of *Quercus*, *Lithocarpus*, and *Castanopsis* of Eastern Asia, with Notes on their Distribution" (see p. 159), and a paper by Professor Sir WILLIAM WRIGHT SMITH and Dr. H. R. FLETCHER, "The Genus *Primula*: Sections *Capitatae*, *Cortusoides*, *Dryadifolia*, *Malvacea*" (see p. 55), were read by title.

JUNE 15, 1944.

Dr. E. WYLLIE FENTON, President, in the Chair.

Mr. KAARE RODAHL read a paper on the Swedish-Norwegian Expedition to North-East Greenland, which he illustrated with coloured lantern slides.

Another paper by the same author, "Content of Vitamin C (1-Ascorbic Acid) in Arctic Plants," was read by title (see p. 205).

TRANSACTIONS
OF THE
BOTANICAL SOCIETY OF EDINBURGH

SESSION CVIII

THE LEAF ANATOMY OF *PODOCARPUS*. By M. Y. ORR.
(With Plates I. and II.)

(Read 11th November 1943.)

In Pilger's review of the Gymnospermae (26), the genus *Podocarpus* is credited with some 70 species, but this number has been considerably augmented by new discoveries in the last two decades, so that, at the present time, *Podocarpus* is one of the richest genera of the Coniferae, and almost coequal with *Pinus* in the number of its recorded species. The great majority of *Podocarpus* species belong to the warm temperate and sub-tropical regions of the southern hemisphere, comparatively few indigenous species being found in countries north of the equator, and none at all in Europe, North America, North Africa or the Orient. Of all the geographical areas in which the genus is represented, South America and Malaya are perhaps the most prolific in point of numbers.

Notwithstanding this wide range of distribution, and the size of the genus, there is remarkable uniformity in the vegetative habits of its members, and but little variation in the form of the foliage, if the dimorphic type peculiar to the few odd species of the section *Dacrycarpus* and the scale-like leaves of *Microcarpus* are excepted. In the great majority of the species the leaves are typically dorsiventral, and the only distinction that can be drawn externally is that between the broad, pluricostate foliage of the *Nageia* species, and the linear or lanceolate, unicostate form of leaf so characteristic of all the species of *Stachycarpus* and *Eupodocarpus*. The leaves vary in length from a few millimetres to as much as 25 centimetres, and are borne either spirally, or in two

opposite ranks on the stem, the former arrangement being by far the more usual in the genus as a whole.

In the absence of the reproductive organs, which serve chiefly to separate the different sections of the genus, it is by no means a simple matter in many cases to identify species of *Podocarpus* with certainty by their vegetative features alone. It is true that the presence of stomata on the upper surface of the leaves serves to separate one group of *Stachycarpus* species from another, and a similar distinction exists in the case of three of the *Nageia* species, but in the much larger section of *Eupodocarpus* the distribution of the stomata has no such diagnostic value, since all the included species, without exception, have hypostomatous foliage. Again, the presence, or absence, of a well-defined midrib may be of some use in separating species, and a midrib that is sulcate above is a feature of considerable value as a species indicator because of its comparative rarity in the genus. On the whole, however, the external characters which may be utilised with certainty for purposes of identification in the case of sterile material are relatively few in number. By having recourse to the leaf anatomy, it has been found possible to supplement the often meagre evidence of identity based on external morphology, and it was with a view to exploring more fully the possibilities of utilising anatomical differences for the solution of taxonomic problems that this investigation of the leaf anatomy of a large number of *Podocarpus* species was undertaken.

Successive plant morphologists have made the comparative anatomy of Gymnosperm leaves a subject of research, but probably the first to attempt to classify species of *Podocarpus* according to their leaf structure was Bertrand (3), who summarised in the form of a key the chief anatomical features of the leaves of thirteen of the better known species of *Eupodocarpus*. He was followed by Mahlert (17), who dealt in a similar way with some fifteen species, taken at random from both *Eupodocarpus* and *Stachycarpus*. Mahlert makes the presence or absence of transfusion tissue and hypoderm the deciding factor in the determination of the species he investigated, whereas Bertrand lays stress on the number and distribution of stomatal lines on the surface of the leaves as a differentiating character, although his assumption that only those species he named are amphistomatous is obviously incorrect.

A more general account of the leaf anatomy of *Podocarpus* is given by van Tieghem (35) in a comprehensive work on the structure and affinities of the different sections of the genus. This investiga-

tion covered some twenty-six recognised species, and these this author has grouped according to the principal anatomical features of the leaves, which they possess in common. *Eupodocarpus* is subdivided into two groups of species: *P. Totara*, *P. falcatus*, *P. nubigenus*, and *P. vitiensis*, for example, being separated from the longer-leaved forms such as *P. macrophyllus* and *P. neriifolius*, which, along with others, are characterised by the presence of a clearly defined "tissu d'irrigation," the term used by van Tieghem to describe the fascia of elongated elements, lying between the palisade and spongy tissues of the leaf. According to van Tieghem, this particular tissue should be regarded, physiologically, as "transfusion tissue," although other anatomists have ascribed to it a purely mechanical function. A brief description of the chief anatomical features of the leaves of four species of the *Nageia* section is also given by van Tieghem, but his statements in this connection are not entirely in accordance with the facts, since, apparently, he was unaware that in the distichous foliage of *P. Blumei* and *P. Wallichianus* the reversed orientation of the leaves of one rank, brought about by the twisting of the petioles, is accompanied by structural differences. What these differences amount to will be explained later in this present paper.

The physiological anatomy of the so-called transfusion tissue, which forms such a striking feature of the leaves of *Podocarpus*, as well as of those of *Cycas*, had been made the subject of detailed investigation by many of van Tieghem's contemporaries, and divergent views had been expressed regarding its exact nature and the purpose it fulfilled in the plant economy. As pointed out by Bernard (2), it is unfortunate that in the writings of earlier workers the term "transfusion tissue" has been used indiscriminately to indicate one or other of two differently placed groups of elements in the leaves of *Podocarpus* species. One is the network of tracheidal cells which is intimately associated with the vascular bundle and is common to the leaves of almost all Gymnosperms; the other is the system of thick-walled, elongated elements which extends outwards from the bundle-sheath, at right angles to the axis of the leaf, and is peculiar to *Podocarpus* and *Cycas*. In descriptions of these tissues, which have appeared from time to time, different interpretations have been placed upon their origin and function, and an involved terminology has grown up around them.

The first mention of the occurrence of pitted cells, forming a fringe round the vascular bundle in *Podocarpus* leaves, was made by Karsten (14) in 1847, and it was to this tissue that von Mohl (19),

believing that in some way it was concerned with the transference of water, gave the name of "transfusion tissue." De Bary (1), who made a more detailed examination of this transfusion tissue, identified the component cells as tracheids, and expressed the view that the "tracheidal seam," as he called it, compensated to some extent for the absence of lateral veins from the conifer leaf. Some time before, Thomas (34) had made a study of the leaf anatomy of *P. macrophyllus* and other species of the genus, and had demonstrated the occurrence of bands of thick-walled, pitted elements, extending through the mesophyll towards the margins of the leaf, and closely resembling those found in the leaflets of *Cycas*. These bands he described as "quergestrecktes Parenchym," thus implying that this tissue is distinct, both in origin and composition, from the tracheidal border of the vascular bundle. Bertrand, whose work has been referred to above, created confusion by applying the term "transfusion tissue" to the so-called transverse parenchyma of Thomas, and he further complicated matters by proposing a different name for the system of tracheids within the bundle sheath. The latter he named the "tissu reticulé," and on its diverse characteristics in certain genera of Coniferae he based a key for their identification. Zimmermann (39), discussing the relationships of the two tissues in question, stressed the point that the transfusion tissue of von Mohl and the transverse parenchyma of Thomas are not connected, but are separated by a layer of parenchymatous cells. He considered the function of the latter to be strictly mechanical, and he therefore restricted the use of the term transfusion tissue to the tracheid mesh within the bundle sheath. Thus the tissue of transfusion bid fair to become the tissue of confusion, owing to the ambiguity attached to the application of the term by successive authors, while the substitution of alternative terms to obviate misunderstanding does not appear to have had the desired result.

Those morphologists, Scheit, Bernard and others, who objected to the misuse of the definition transfusion tissue, and advocated its disuse in this connection, were influenced in their choice of other distinctive terms by their individual impressions of the physiological purpose of the tissues concerned. As might be expected, no general agreement on the debatable question of function was reached. Among those who regarded the so-called "transverse parenchyma" as fulfilling a purely mechanical purpose in strengthening the lamina of the leaf are Zimmermann and Mahlert, the latter postulating a close analogy between the isolated thick-walled elements

of the mesophyll in the leaves of *P. alpinus* and *P. nivalis* and the stellate fibres in the cladodes of *Sciadopitys*. Incidentally, had the species, then undescribed, been known to him, Mahlert might have found in the multiradiate sclereids of *P. Ladei* and *P. ferruginoides* a more striking parallel. In opposition to the mechanical theory, a number of investigators, like van Tieghem and Scheit, held the view that the special construction of the transverse parenchyma was more suggestive of conduction, and might possibly be connected with the transpiratory activity of the leaf, which, according to Scheit (28), who investigated its physiological anatomy, is the chief factor determining the quantitative development of transfusion tissue in general.

In a paper on the origin and function of transfusion tissue Worsdell (37) formulated the theory that the tracheidal cells within the bundle sheath had been derived phylogenetically from pre-existing centripetal xylem, and he suggested further that the strands of lignified elements in the mesophyll should be regarded as lateral extensions of the xylem, originating from the same source. In order to remove any further ambiguity arising out of the use of the term transfusion tissue as a name for the latter, Worsdell designated it "accessory transfusion tissue," although he did not seek to imply thereby that a water-conducting function is preserved. Rather does he appear to incline to the view held by Zimmermann and Mahlert that this tissue now plays only a mechanical part in giving strength to the leaf blade, and he cites as evidence of its vestigial nature the absence of an organised accessory transfusion tissue from the leaves of certain small-leaved species, such as *P. alpinus*, where it is represented by isolated stereids. These "stone-cells" Worsdell regards as relics of the well-developed tissue seen in *P. chilinus* which, in *P. alpinus*, has become superfluous owing to the reduction in size of the leaves. Worsdell's statement that there is only slight lignification and an absence of pitting in the mesophyll cells of *P. Totara* is not strictly correct, for in the leaves of this species, and in those of its close ally *P. Hallii*, lignification and pitting of the walls of mesophyll elements is clearly visible. This is confirmed by Pilger (26), who, however, considers these lignified cells in the leaves of *P. Totara* and *P. alpinus* to be merely modified parenchymatous elements. Furthermore, Worsdell's assumption that the isolated stereids in the leaves of *P. alpinus* are vestigial structures is scarcely in keeping with the fact that homologous elements occur sporadically in the mesophyll of many Podocarps which possess also a typical accessory trans-

fusion tissue. The present writer has observed similar lignified cells with non-bordered pits and wide lumen in the leaves of various species, often interspersed among the cells of the palisade layer and frequently in contact with the hypoderm, but usually separated from the accessory transfusion tissue, of which Worsdell would regard them as relics. No doubt, by reason of their structure and situation, such elements have the effect of lending support to the leaf, although adequate protection of the tissues would seem to be ensured by the presence of a sclerosed hypoderm. Whatever part these sclereids play in the plant economy, the fact remains that their constant occurrence in the leaves of certain species of *Podocarpus*, and their absence from others, makes them of some diagnostic importance in the identification of species.

In a lengthy paper, published in 1904, Bernard (2) gives a very complete summary of the work done in this field up to that time, and he also contributes further valuable observations of his own on the nature of transfusion tissue in Gymnosperm leaves in general. Following Worsdell, he elaborates the theory that the isodiametric tracheids bordering the vascular bundle represent centripetal xylem, and in species of *Podocarpus* from which the accessory transfusion tissue is absent these may extend far out into the mesophyll. Bernard viewed with disfavour the continued misuse of the term transfusion tissue by successive authors, and in place of it he proposed a new term "hydrostéréome transversal." He pointed out that the "hydrostéreids" of which this tissue is composed vary in character according to the size and age of the leaves, and may be absent from those of young plants of *Podocarpus* in which they are found normally at maturity. He suggested that the hydrostereome might perhaps be a continuation of the centripetal xylem, but acting more as a supporting tissue, and in this respect resembling the stellate idioblasts found in the leaves of *Agathis loranthifolia* and *Sciadopitys verticillata*. As a result of his investigations, Bernard came to the conclusion, to quote his own words, "qu'il est possible de faire des distinctions entre les différentes espèces, selon les caractères de l'hydrostéréome transversal et du bois centripète," but the use he made of these characters in his scheme of classification serves to separate groups of species rather than to distinguish individual species.

Since Bernard's time the leaf anatomy of the Podocarps has not attracted the attention of morphologists to the same extent as before, and the number of contributions to the subject which have appeared in the intervening years is comparatively small, while

few of the writers treat the subject from a taxonomic standpoint. In 1912, Stiles (33) published a paper on the comparative morphology of Podocarpeae, in the course of which he reviews, in a general way, the anatomical features of several well-known types, as exemplified by *P. macrophyllus*, *P. salignus*, *P. vitiensis*, and *P. nagi*, but he adds little that is new to what is already known of the leaf anatomy of these species. In an earlier work this author, in collaboration with Brooks (5), had dealt with the general morphology of *P. spinulosus*, but only a very brief account of the features of the foliage is included.

In a treatise on the anatomy and biology of Gymnosperm leaves, which appeared in 1921, Feustal (8) makes frequent references to species of *Podocarpus* when describing the principal tissues met with in the leaves of members of the Taxaceae. He quotes extensively from the works of previous authors, but, unlike Bernard, he does not believe that true centripetal xylem is to be found in the leaves of *Podocarpus*. He follows Worsdell, however, in drawing a sharp distinction between the abbreviated sclereids, such as those found in the mesophyll of *P. alpinus*, and the elongated elements which form the accessory transfusion tissue in other Eupodocarpus species.

In an interesting paper on the development of the leaves of some New Zealand conifers, Griffin (13) traces the formation of the lignified cells with simple pits in the mesophyll of *P. Totara*, and states her belief that these elements undoubtedly function as a transfusion tissue, in conveying water to the margins of the leaf. These cells, Griffin points out, are in no way different morphologically from those in the leaves of *P. alpinus*, described as "stone cells" by Worsdell. Miss Griffin gives descriptions also of the leaves of *P. ferrugineus* and *P. spicatus*, which are alike in one respect that neither hypoderm nor organised accessory transfusion tissue is present, although she indicates that there are elongated cells on either side of the vascular bundle in the leaves of *P. spicatus*, which have slightly lignified walls and are pitted. On the important question of the origin of transfusion tissue this authoress is at variance with Worsdell, for she holds the opinion that, in the leaves of the species she had examined, the elements of the accessory transfusion tissue are formed from modified parenchyma and do not represent centripetal xylem. On this point she is in agreement with the conclusions reached by Thomas.

Of the more recent works dealing, incidentally, with *Podocarpus*, that of Ziegenspeck (38), on the needles of seedling and adult

conifers, merits no more than a passing mention, for it contains merely a brief survey of the salient features of the leaf anatomy of five species of *Podocarpus*, all of which had been described already in the works of previous authors.

Florin's (9) extensive researches on epidermal structures in the leaves of Gymnosperms, ancient and modern, belong to a different category, and his descriptions of the diverse characters of the stomatal apparatus in the various genera, including *Podocarpus*, have a positive value for the systematic botanist as well as for the morphologist.

Florin's investigations cover all the species of *Podocarpus* then known, and in each case the structural details of the stomata and configuration of the epidermal elements are described with meticulous care. Each section of the genus is treated separately, and the included species are grouped, where it is possible, according to the disposition of the stomata and the nature of the adjacent tissue. Thus, in *Stachycarpus*, the species fall naturally into two groups: those with stomata mainly on the under side of the leaves, and with palisade tissue more or less well defined; and those with stomata on both surfaces of the leaves, which show but little distinction internally between the upper and lower sides. The section *Nageia* is similarly subdivided into two groups: *P. Blumei*, *P. Motleyi* and *P. Wallichianus* being amphistomatous, whereas *P. nagi*, *P. nankoensis* and *P. formosensis* are hypostomatous. The former group has a much wider geographical range than the latter, which is confined to southern Japan and Formosa. Florin points out that the division of this section into two groups of species, one amphistomatous and the other hypostomatous, corresponds with Pilger's classification which is based on the presence or absence of a receptacle in the female "flower," this structure being well developed in *P. Motleyi*, *P. Blumei*, and *P. Wallichianus*, and absent from the hypostomatous species.

The section *Polypodiopsis*, established by Bertrand to include the anomalous species *P. vitiensis*, is revived by Florin, and to it he has relegated *P. Rospiglosii*, which has much in common with *P. vitiensis*, and *P. minor*, which had been placed by Pilger in the *Nageia* section. In these three species, the leaves are amphistomatous, but the number of resin canals varies, there being several in the first two species according to Florin, and one only in the leaves of *P. minor*.

In *Eupodocarpus*, Florin states, structural differences in the epidermal tissue are not pronounced, and from the standpoint of

its leaf anatomy he regards this section, as at present constituted, a reasonably natural unit.

The latest reference to distinguishing characteristics in the foliage of *Podocarpus* species is that contained in a paper by Roberts and Doyle (27), on the pH of conifer leaves, and although in this case it is the chemical properties, and not the anatomical features, that form the basis of species analysis, this work is noteworthy because it is an illustration of ultra-modern methods of determining specific relationships. Twelve species of *Podocarpus* were examined and were classified according to the relative acidity of the cell-sap in their leaves, and the results, expressed in tabular form, show that *Podocarpus* possesses a greater pH range than any other genus of the Coniferae. There are indications of the segregation of species into distinct pH groups, and the high acidity of the foliage of *P. andinus* is a fact which the authors regard as being of considerable interest in view of the widely held opinion that this species should be excluded from the genus because of differences in the reproductive organs. A recent statement by Briggs (4) on the isolation of phyllocladene from *P. Hallii* is also significant on account of its bearing on inter-specific differences.

A review of the literature dealing with the leaf anatomy of *Podocarpus* makes it clear that out of the very large number of species only a relatively small proportion of these has been studied, and a comprehensive account of the structure of the leaves throughout the genus as a whole is lacking. Moreover, much of the excellent research that has been carried out in the past has been concerned primarily with the problem of the transfusion tissue, its nature, origin and function, while the possibility of utilising the peculiarities of the general leaf structure for diagnostic purposes has not been fully explored. Not infrequently, for the identification of sterile material of *Podocarpus* species, the writer has turned to the leaf anatomy for enlightenment when other data have failed to provide conclusive evidence of identity, and it was in order to ascertain how far structural differences between species could be relied upon as distinguishing marks that a study of the leaf anatomy of all the available species was undertaken. Since the species included in *Dacrycarpus* and *Microcarpus*, with needle-like and scale-like foliage, do not present the same difficulties of identification, they were excluded from the investigation, which was confined to the flat-leaved species comprising the sections *Stachycarpus*, *Eupodocarpus*, *Nageia* and *Polypodiopsis*. The results of this work, it was thought, might show also to what extent leaf

anatomy is indicative of specific affinities within the sections, and how far it represents a response to external ecological factors.

The material employed for this purpose was taken chiefly from duly authenticated herbarium specimens from native sources, but, where possible, comparisons were made with the leaves of species in cultivation, and any inconsistencies in the structure of the latter, due to growth in an artificial environment, were duly noted. Quite a number of interesting facts came to light in this way. Altogether, some 70 species of *Podocarpus* were examined from the point of view of their leaf anatomy, a number of the rarer and more recent species being of necessity omitted, as specimens of these were not readily obtainable at the time.

Much of the material employed in this investigation came from the Herbarium at the Royal Botanic Garden, Edinburgh, but the writer is also indebted to the Director of the Royal Botanic Gardens, Kew, and to the Keeper of the Herbarium at the Natural History Museum, South Kensington, for the loan of specimens unobtainable at Edinburgh, and he welcomes this opportunity of recording his appreciation of the readiness with which these authorities placed suitable material at his disposal. Living specimens of species not in cultivation at Edinburgh were obtained also from Kew, as well as from the Botanic Garden at Glasnevin, Dublin, and for the material supplied from these sources the writer desires to express his thanks. Leaves from herbarium material and cultivated plants selected for microscopic examination were sectioned by hand after suitable treatment, and a special word of commendation and thanks is due to Miss E. Stott of the Laboratory Staff at Edinburgh for the preparation of the very excellent leaf sections used for this investigation.

In the account of the leaf anatomy of *Podocarpus* species which follows, each section of the genus is treated separately, and the grouping of the species, with some slight modifications, is based on Pilger's Monograph of the Taxaceae (25).

STACHYCARPUS Endl.

The section *Stachycarpus*, which some continental systematists consider should rank as a sub-genus, includes those species of *Podocarpus* of which the female "flowers" are borne, several together, in a spiciform arrangement, and where there is no subsequent development of a fleshy receptacle below the seed, as is the case in other sections of the genus. *Stachycarpus* is a relatively small

section, comprising only 17 species,* which are widely distributed throughout the continental areas and islands of the southern hemisphere, very few of them being found north of the equator. On morphological grounds, the species are separated into two groups, each of which, according to Florin (9), might well be raised to the status of a section, comparable with the other well-established subdivisions of the genus.

The first group consists of species the adult foliage of which is for the most part hypostomatous, and includes *P. andinus* Poepp. (Chile), *P. Harmsianus* Pilg. (Colombia, Venezuela), *P. montanus* Lodd. (Colombia, Venezuela, Peru, Bolivia, Costa Rica), *P. utilior* Pilg. (Peru), *P. ferrugineus* D. Don, *P. spicatus* R. Br. (New Zealand), *P. Ladei* Bailey (Queensland), *P. amarus* Blume (Queensland, Philippines, New Guinea, Java, Sumatra), *P. glaucus* Foxw. (Philippines), *P. ferruginoides* Compton (New Caledonia), *P. rostratus* Laurent (Madagascar). Although the majority of these are characteristically hypostomatous, *P. ferruginoides* and *P. Ladei* are exceptional in having stomata on both sides of their leaves, while occasionally a few stomata may occur sporadically on the upper surface of the leaves of *P. amarus*, *P. andinus* and, according to Griffin (13), *P. ferrugineus* also.

The second group comprises those species the adult foliage of which is invariably amphistomatous, and a small amount of palisade parenchyma is produced on both sides of the leaves, the petioles of which are twisted so that the morphological under side is exposed to the light. In none of the species included here is accessory transfusion tissue developed in the leaves. In this group are placed *P. Dawei* Stapf, *P. falcatus* (Thunb.) R.Br., *P. gracilior* Pilg., *P. gracillimus* Stapf, *P. usambarensis* Pilg., all indigenous to Africa, and *P. Mannii* Hook. f., a native of the Island of St. Thomas in the Gulf of Guinea. In their leaf anatomy the species of this second group are singularly uniform, in marked contrast to those of the previous group, which are characterised by a surprising diversity of leaf structure. It is worth noting, in passing, that the leaves of the species forming the two corresponding groups into which the section *Nageia* is divided provide a similar contrast in their leaf anatomy.

Geographically, the species in the first group are widely spread, and diversity of features is to be expected. The African species of

* *P. ulgurensis* Pilg., recorded from Tanganyika, the female strobile of which is unknown, may possibly belong to *Stachycarpus*, but no material of this species is available for examination.

the second group, on the other hand, form a compact and morphologically homogeneous unit, and are obviously closely related. The contrasting features of the foliage of these two groups of species will become apparent when the general features of the leaf anatomy of the component species are described in detail. The writer has been unable to obtain material of either *P. rostratus* or *P. utilior*, and all references to the leaf anatomy of the former are taken from the original description of that species (16). *P. utilior* is said to be akin to *P. montanus*, but the leaves, which are about the same size in both species, are not distinctly grooved on the upper side of the midrib, as they are in the latter species.

A study of the leaf anatomy of the species of *Stachycarpus* has brought to light several features not previously noted, some of which no doubt owe their presence to the operation of environmental factors, while others conceivably may be regarded as forming an integral part of the specific constitution, and as such are therefore of some diagnostic importance. In the first group of species, almost every possible combination of anatomical features is represented in the leaves, and it cannot be said in every case that the features displayed are a response to external influences.

The foliage of the species in this group consists for the most part of relatively small, unicostate leaves, those of *P. ferruginoides*, *P. spicatus* and *P. utilior* being generally no more than 15 mm. in length. *P. amarus* is exceptional in having leaves which are normally 6–8 cm. and occasionally as much as 16 cm. in length. In this species the midrib of the leaves is grooved on the upper side, and there is a similar but less obvious median indentation in the leaves of *P. montanus*. As very few species of *Podocarpus* have leaves with a sulcate midrib, this feature has a definite diagnostic value when it occurs. It has been already pointed out that, with the notable exceptions of *P. ferruginoides* from New Caledonia and *P. Ladei*, a native of Queensland, the stomata are normally confined to the lower surface of the leaves. Reports of the appearance of stomata in the upper epidermis of the leaves of the other species refer to casual occurrences and to the condition in young leaves and cotyledons.

The stomata and the contiguous epidermal elements have been fully described by Florin (9). From the writer's own observations, cutinisation of the epidermis is particularly heavy in *P. ferrugineus*, *P. ferruginoides*, *P. glaucus*, and *P. montanus*, and moderately strong in the remainder of the species in this group. In *P. ferrugineus* and *P. Ladei* the cuticle is corrugated externally, while in *P. fer-*

ruginoides and *P. montanus* the cuticular substance bulges inwards and invades the epidermal cells, tending to obliterate the cell cavities. A similar invasion of the epidermal elements takes place in the leaves of *P. spicatus*, but here it is much less obvious. In the leaves of *P. andinus* and *P. ferrugineus* the inner walls of the cells composing the epidermis are noticeably thickened, while in *P. Harmsianus* the lateral walls as well as the inner walls are so strongly thickened that the epidermal tissue is a most conspicuous feature of the leaf section. In none of these species is there any approach to the formation of a hypodermis, and in fact this tissue is represented in the leaves of two species only in the first group. In *P. rostratus*, according to Laurent, there is an uninterrupted layer of hypoderm, which is sometimes double, on the upper side of the leaves, and there are fibres on the under side also, below the resin ducts and between the stomata. The other exception is *P. glaucus*, in the leaves of which a few large and more or less isolated fibres are found in contact with the upper epidermis, and thick-walled cells of a smaller size form a short continuous layer on the lower side, extending over the midrib, but not into the stomatal region. The possession of a continuous hypodermis renders *P. rostratus* unique among the species of this group, and makes it easy to identify it anatomically by its leaves. Similarly, the presence of isolated fibres occupying the position of a hypodermis in the leaves of *P. glaucus* will act as a clue to the identity of this species. In the leaves of both species, lignified cells with pitted walls are also to be seen in varying numbers round about the vascular bundle.

It may be appropriate at this point to make reference to the peculiar idioblasts found in the leaves of *P. ferruginoides*. These are much larger than the cells of the mesophyll, among which they occur sporadically, and are most curiously branched, resembling to some extent the stellate fibres in the cladodes of *Sciadopitys*. They have enormously thickened walls, visibly striated and pierced with simple pits, and a large lumen. Irregularly shaped fibres of a similar nature are found in the leaves of *P. ferrugineus* and *P. Ladei*, but they are few in number by comparison, much less frequent in their occurrence, and they never attain the prominence of those in the leaves of *P. ferruginoides*, where their diagnostic value is considerable.

Palisade tissue, from two to four cells in depth, is formed below the upper epidermis, and extends across the midrib, in the great majority of the species in this group. Only in *P. Harmsianus* is

this tissue feebly developed, although in *P. ferrugineus* it is ill-defined and loosely arranged, consisting of cylindrical and isodiametric cells intermixed. In both *P. ferruginoides* and *P. Ladei*, on the other hand, despite the presence of stomata in the upper epidermis, the palisade tissue lying beneath is well organised and compact. As all the species in this group possess leaves of the bifacial type, no diagnostic importance can be attached to the palisade tissue, and, in any case, it is a variable feature, as is shown by its unequal development in sun and shade leaves. Below the palisade tissue lies the spongy parenchyma. This presents no unusual features, except that most of the cells in this region in the leaves of *P. montanus* have thick walls.

Between the palisade tissue and the spongy parenchyma lies the so-called "transverse parenchyma," the accessory transfusion tissue of Worsdell. This tissue, which is such a common feature in the leaves of the species of Eupodocarpus, is present in only three of the species of Stachycarpus. These are *P. amarus*, a species with a wide distributional range extending from Queensland to the Philippines, *P. glaucus*, also a native of the Philippines, and *P. rostratus*, a species indigenous to Madagascar. Although spatially separated, these species possess in common this special feature, not shared by their immediate congeners, and if further evidence of their distinctness is required, it is furnished by the fact that in the leaves of each of these three species there are three resin canals below the vascular bundle, whereas in those of all the other species of the group there is only one canal. It is unwise to attach undue importance to the value of anatomical features as indicators of affinity, but such deep-seated characters as those mentioned above must surely form parts of the specific constitution in each case, and their presence in the leaves of these three species is but another instance of the composite nature of the group. The composition of the accessory transfusion tissue, and the possible function it fulfils in the economy of the plant, have been fully discussed already in this present paper, therefore it is unnecessary at this point to do more than refer to it in general terms. This tissue is especially well developed in the leaves of *P. amarus*, and here, as in the other species, it is composed of the characteristic elongated elements with lignified and pitted walls, which are separated from the tracheids bordering the vascular bundle by the interposition of the living cells of the bundle sheath. The transfusion tissue proper, within the bundle sheath, is well represented generally in the species of this group. It is particularly prominent in the leaves of *P. amarus*,

but in those of *P. ferrugineus* it is inconspicuous and is reduced to a few tracheids on each side of the bundle.

Situated below the phloem of the vascular bundle in the leaves of all *Podocarps* there is one or more resin canals of variable size, the actual number of these present in the leaves of different species being an important factor in their identification. Reference has been made to the variation in number of the canals found in the leaves of the species in this group, and it is interesting to note that three resin ducts are present in only those with accessory transfusion tissue. This association of anatomical features belonging to different categories is probably without significance, since many *Eupodocarpus* species with accessory transfusion tissue in their leaves possess only one canal. Nor, in the present case, is the size of the leaves likely to be the determining factor in the production of three resin canals, for, though the leaves of *P. amarus* are long and comparatively broad, those of *P. glaucus* are not larger than the leaves of other species in which a single duct is normally found. Where three resin canals are present in the leaves, the central duct is usually the widest, and in *P. amarus* in particular it is so conspicuous a feature of the leaf section that the lateral canals, when not fully developed, are apt to be overlooked. This may account for van Tieghem's erroneous statement that in this species there is only a single dorsal canal (35).

It is evident, from this analysis of the leaf anatomy of these species, that *P. amarus*, *P. glaucus* and *P. rostratus* stand alone as regards the structure of their leaves, and there is something to be said for their segregation in a special group, apart from the other species with which they are commonly allied.

The species of *Stachycarpus* with universally amphistomatous foliage do not show that diversity of structure in their leaves which characterises the species just described, and they have every appearance of being a compact group of closely related forms. In fact, so homogeneous are they in their leaf morphology that identification by means of their anatomy is rendered almost impossible. Before proceeding to give a description of the structural features of their leaves, however, it will be necessary to preface it with some notes on the species and their distribution.

There are six species in this group, five of which, it has been already mentioned, are confined to the African continent and one to an island in the Gulf of Guinea. They are thus geographically remote from all the other species in this section, the nearest point of contact being with *P. rostratus* in the island of Madagascar.

The species with the most southerly distribution in this group is *P. falcatus*, a native of the Cape, Natal and the Transvaal. It has been recorded also from British Bechuanaland and Portuguese East Africa. One of the synonyms of *P. falcatus* is *P. elongata*, a name proposed by Carrière, and in consequence this species has often been confused with *P. elongatus* of L'Héritier, which is also indigenous to South Africa, but belongs to the section Eupodocarpus. As an instance of the way in which these names have been misapplied there appears in Bernard's work on the leaves of the Coniferae (2), a text-figure portraying the leaf anatomy of L'Héritier's species, which is wrongly labelled "*P. falcatus*." As the structure of the leaves in these two species is entirely different, this error in nomenclature is most misleading. Two other species in this group occur in the Transvaal. These are *P. gracilior*, which has an extended range throughout eastern tropical Africa as far north as Abyssinia, and *P. gracillimus*, which Stapf (32) has suggested may represent merely a form of *P. gracilior* with shorter and narrower leaves. According to the same authority, it is possible that *P. falcatus* and *P. gracilior* may be geographical varieties of a hypothetical composite species. Certainly the leaf anatomy of these three species postulates a very close affinity. *P. Dawei*, a native of Uganda, closely resembles the foregoing also in the form of its foliage and the structure of its leaves. *P. usambarensis*, with much longer leaves, which approximate anatomically more nearly to those of *P. Mannii*, is indigenous to Tanganyika, and is a dominant species, along with *P. milanjanus*, of the open type of *Podocarpus* forest at 1900–2500 m. in West Usambara. All are tall trees, with flat, linear leaves, which vary in length from 3 or 4 cm. in *P. Dawei*, *P. falcatus*, and *P. gracillimus* to 8 cm. in *P. gracilior* and *P. usambarensis*, and are crowded towards the end of the branches in the adult state. The remaining species of this group is *P. Mannii*, endemic in the island of St. Thomas, with much longer leaves, up to 16 cm., and 1 cm. in breadth, not differing greatly from those of the other species in their general anatomy.

Anatomically, the leaves of all the species mentioned above have much in common, and they are quite unlike those of the previous group of species, for, in addition to being consistently amphistomatous, the leaves are uniformly isobilateral, with palisade tissue on both sides. It has been demonstrated by Seybold (31), using *P. Mannii* as an example, that the arrangement of the leaves in two regular rows on the plagiotropous shoots is brought about by internodal torsion of the branches, and this is followed by a twisting

of the leaf stalks, which has the effect of reversing the orientation of the leaves in one rank, so that the morphologically under-surface becomes exposed to the light. It was subsequently pointed out by Kugler (15) that the palisade tissue on the illuminated side of the isobilateral leaves is actually greater in amount than on the shaded side, this quantitative differentiation, not foreshadowed in the bud, being due directly to the influence of light, and can be observed in young leaves after a few months. The leaf anatomy of *P. Mannii* had already been investigated by Nobre (20), but his account deals chiefly with the tissues of the midrib, and contains no reference to the palisade parenchyma and the inequalities described by Kugler. A hypodermis is present in the leaves of all the species in this group, and, except at the margins of the leaves, and above and below the vascular bundle in one isolated case, it is always discontinuous, the fibres composing it being arranged in short rows, or in isolated groups which often jut out into the underlying parenchyma. Strengthening fibres also encircle the vascular bundle, and are dispersed through the adjacent mesophyll, giving a most characteristic appearance to sections of the leaves of these species.

There is no accessory transfusion tissue in the leaves of any of these species, and, in place of it, the tracheidal tissue bordering on the vascular bundle is extended outwards into the mesophyll for some distance on both sides. The elements of which this tissue is comprised have lignified walls with simple pits, similar to those which form the accessory transfusion tissue in the leaves of *P. amarus*, but they differ in not being prosenchymatous. The extension of the transfusion tissue proper beyond its normal limits is an unusual feature, found only in these species of *Stachycarpus* and in those of the next section, and it is difficult to explain why it should be restricted solely to these particular species, unless it happens to be a sign of primitiveness. It will be recalled that Worsdell formulated the theory that transfusion tissue in the leaves of conifers is derived, phylogenetically, from the centripetal xylem of some ancestral type, and, if that is so, its survival in this exaggerated form in the leaves of these *Podocarpus* species might be regarded as an indication of the comparative primitiveness of the groups to which they belong.

This enumeration of the anatomical features common to the leaves of these six species of *Stachycarpus* will suffice to show how closely the leaves conform to one particular pattern, which has the quality of a "family likeness," and is suggestive of the common

origin of all the species in this group. Individual specific differences do exist, but these are scarcely positive enough to be of diagnostic importance, except perhaps in one or two special cases, such as that furnished by the distinctive character of the mesophyll in the leaves of *P. Mannii* and *P. usambarensis*. In these two species a large number of the cells which form the ground tissue of the lamina, lying between the upper and lower palisade layers, are devoid of living contents, and have lignified walls provided with simple pits. These sclerenchymatous elements may be slightly elongated in a transverse direction, but they have a wide lumen and are quite unlike the elements which form the accessory transfusion tissue of other species, although, in the aggregate, they probably perform the same function by giving strength and rigidity to the leaves. Lignified cells of a similar nature are seen sometimes in sections of the leaves of *P. Dawei* and *P. falcatus*, and more frequently in those of *P. gracilior* and *P. gracillimus*, but in none of these are they so numerous, or so conspicuous, as they are in *P. Mannii* and *P. usambarensis*. It is significant that in the leaves of these two species, which are longer and broader than those of the majority of species in this group, the extension of the transfusion tissue into the mesophyll is very much reduced.

Reference has been made to the general construction of the hypodermis, and although there is a certain amount of variation in the size and arrangement of the individual fibres in the species of this group, the differences observed are, for the most part, never sufficiently obvious, or consistent enough, to provide a means of distinguishing one species from another. There are, however, one or two cases where the character of the hypodermis might afford a clue to the identity of the species. In the leaves of *P. falcatus*, for instance, the hypodermal fibres are much larger than those of any other species, and the groups into which they are segregated project more deeply into the underlying mesophyll. Again, in the leaves of *P. Mannii* and *P. usambarensis*, the hypodermal layer has the appearance of being interrupted at greater intervals than is usual in the other species, and in the region of the midrib in *P. usambarensis* it forms an unbroken layer above and below the vascular bundle. The fibrous elements of the ground tissue contiguous to the vascular bundle also differ appreciably in size according to the species, and it is noteworthy that they reach their greatest dimensions in *P. gracillimus*, the leaves of which are narrower than those of any other species in this group. In this case the fibres have an exceptionally thick, stratified wall and a small lumen.

These are, individually, small points of difference, but when taken in conjunction with other features they may become deciding factors in the identification of the species. It should be obvious, however, that the validity of such distinguishing marks can only be tested by examining and comparing a considerable number of leaf sections, since xeromorphic characters in particular, according to Zalensky, tend to vary, and are more pronounced in the leaves borne on the upper branches than in those produced lower down on the tree.

From this detailed account of the leaf anatomy of the species included in *Stachycarpus* it will be seen that the two groups into which the section is divided are anatomically distinct, those of the first group being characterised by an admixture of various types of leaf structure, exhibiting features which are capable of being utilised for identification purposes, while those in the second group, because of their close kinship, conform to one type of leaf structure, and this shows so little variation in its characters that only in a few cases is it possible to separate species on anatomical grounds.

It has been suggested that the first group might be subdivided into two smaller groups of species to include those with, and those without, accessory transfusion tissue in their leaves. The former, in which the resin canals are three in number, can be distinguished individually by the presence of a hypodermis, continuous in *P. rostratus* and discontinuous in *P. glaucus*, or by its total absence from the leaves of *P. amarus*, which are sulcate on the upper surface. Among the species without accessory transfusion tissue in their leaves, and with one resin canal only, *P. ferruginoides* and *P. Ladei* are exceptional in having stomata on both upper and lower surfaces. These two species may be distinguished individually by the occurrence of idioblasts in the mesophyll, these objects being very numerous in the former and much less so in the latter species. The peculiar formation of the cuticle is also a specific mark of *P. ferruginoides*. Stomata are to be seen occasionally on the upper surface of the leaves of *P. andinus* and *P. ferrugineus*, but in the case of these two species the structure of the epidermal cells, the inner walls of which are visibly thickened, provides a means of identifying them. *P. ferrugineus* can be distinguished from *P. andinus* by its thicker, indented cuticle, the feebly developed palisade tissue, and by the casual occurrence of idioblasts in the ground tissue of the leaves. The structure of the epidermis is also a diagnostic feature of the leaves of *P. Harmsianus*, the lateral walls, as well as the inner wall of the cells composing it, being strongly

thickened. Finally, *P. montanus* is separable from *P. spicatus* by the greater breadth of its leaves, which are slightly grooved above in the median line, and anatomically by the thickened walls of the mesophyll elements, and the relatively deep palisade tissue, more apparent in native specimens. On the other hand, the lower epidermis of the adult leaves of *P. spicatus* is noticeably papillate when seen in section, whereas that of *P. montanus* is generally smooth.

It is remarkable that the leaf anatomy of one group of *Stachycarpus* species should be so complex, and that of the other group so uniform, when the fundamental characters of the reproductive organs are essentially the same in all the species. It cannot be said that the diversity of structure seen in the leaves of species belonging to the first group is due in every case to the action of ecological factors. Doubtless, some of the superficial features of the leaves, such as the development of cuticle, represent responses to environmental conditions, but it is unlikely that accessory transfusion tissue belongs to this category, and its presence in the leaves of three of the species of this group would seem to postulate for these at least a separate origin.

POLYPODIOPSIS Bertrand

Originally established by Bertrand (3) to include a single species, *P. vitiensis*, a native of Fiji, with opposite leaves, flattened in one plane, and possessing distinctive features in the reproductive parts, the section *Polypodiopsis* has been enlarged by Florin (9) to embrace two other species, *P. minor* (Carr.) Parl., belonging to New Caledonia, and *P. Rospighiosii* Pilg., a Peruvian species, recorded also from Colombia and Venezuela. Both *P. vitiensis* and *P. minor* are considered by Pilger (26) to be doubtfully akin to the species of the *Nageia* section, but the leaves are unicostate, whereas those of the *Nageia* species are pluricostate, and the male strobile of the former species does not agree. The position of the female strobiles in *P. vitiensis* led Gibbs (11) to place this species in *Stachycarpus*, with which the male reproductive organs do agree, and a further point in favour of this view is the approximation of this species to *P. ferrugineus*, not only in habit and appearance, but also in the positions of the male and female strobiles. Subsequent investigation by Gibbs (12) on the nature of the female reproductive organ, not previously available, caused this authoress to change her opinion, and to leave *P. vitiensis*, provisionally, in *Nageia*, although, as she has pointed out, the very characteristic branching of the

peduncle and other peculiar features of the female organ have no counterpart in any other section. For this reason the present writer has adopted Bertrand's original classification of this species, despite some doubt regarding the correctness of all the characters upon which it is based. Notwithstanding the claim put forward by Florin for the inclusion of *P. minor* in *Polypodiopsis*, the systematic position of this species is still uncertain, in view of the present lack of knowledge regarding the true nature of the female reproductive organ. In the morphology of its vegetative parts, and especially in its leaf anatomy, *P. minor* bears some resemblance to species of *Stachycarpus*, such as *P. falcatus*. But the same may be said of *P. vitiensis* also, and this will become apparent when the structure of the leaves of both species is described. The association of *P. Rospigliosii* with *P. vitiensis* is natural, because of the similarity of their vegetative parts, although the female "flower" of the former species is as yet unknown. The writer has had no opportunity of examining the type specimen of *P. Rospigliosii*, and all references to the leaf anatomy of this species are based on other material of this species, not quoted by Pilger in the original description.

In the general morphology of their foliage, such as the arrangement of the two-ranked leaves in one plane, the reversed orientation of the lamina, and the distribution of the stomata over both surfaces of the leaves, all three species are alike in their resemblance to those of the second group of *Stachycarpus*. The process of internodal torsion, by which the bilateral symmetry of the plagiotropous shoots is achieved in *P. Mannii*, is repeated in *P. Rospigliosii*, and has been demonstrated diagrammatically by Florin (9) (figs. 51, 52) in the case of the latter species. The leaves are similarly twisted at their base, and in those on one side of the shoot the morphologically under-surface becomes uppermost. In their leaf anatomy, also, the species included in *Polypodiopsis* have many points in common with those of *Stachycarpus*. The amphistomatous leaves are of the isobilateral type, with palisade parenchyma developed on the two sides, but sometimes, as in *P. Mannii*, in greater quantity on the illuminated side. In each leaf there is a single vascular bundle, flanked by transfusion tissue, which is extended laterally into the mesophyll in a manner reminiscent of the condition prevailing in the leaves of *P. falcatus* and its near allies. As already pointed out, this rare feature is found only in species belonging to *Stachycarpus* and *Polypodiopsis*. As might be expected, there is no formation of accessory transfusion tissue here, but there is a development of thick-walled cells with wide lumen in the mesophyll

of both *P. minor* and *P. vitiensis*, similar to those found in the leaves of *P. usambarensis* but not in such quantity. No lignified elements of this kind have been detected in the mesophyll of *P. Rospiglosii*, and it is interesting to note that the production of hypodermal fibres in the leaves of this species is much greater than in those of the other two Polypodiopsis species. In *P. Rospiglosii* the hypodermis consists of short rows of fibres between the stomata on both sides of the leaves, and uninterrupted layers above and below the vascular tissue, as well as at the leaf margins. In *P. minor* the hypodermal fibres are larger in diameter but fewer in number and they are often isolated, while in the leaves of *P. vitiensis* this tissue is virtually non-existent, being represented only by occasional fibres of insignificant size, occurring singly or in short rows as at the margins. Strengthening fibres are present also in the parenchyma of the leaves, and in *P. minor* these form disconnected bands above the vascular bundle, an arrangement similar to that in the leaves of *P. falcatus*. A smaller number of fibres occur usually in the same position in the leaves of *P. Rospiglosii* and *P. vitiensis*, but in the latter species their place may be taken by sclerenchymatous cells with wide lumen, corresponding to those found in the mesophyll. Finally, it should be noted that the cuticle on the leaves of *P. minor* is more highly developed than in either of the other two species, and, further, that the epidermal cells of this species are rich in tannin content.

It will be seen, from this brief description of their leaf anatomy, that, up to a point, the leaves of the Polypodiopsis species are essentially similar in their construction to those of the species in the second division of Stachycarpus, and unless this similarity is due to parallel development, which is unlikely in the circumstances, it would seem to suggest a closer relationship between the two sets of species than is implied by their present taxonomic position. The possession in common of that unique feature, a lateral extension of the transfusion tissue, is, by itself, a sign of their close affinity.

No mention has yet been made of the occurrence of resin-canals in the leaves of Polypodiopsis species, and it is on this point that the observations of the present writer are at variance with the findings of other authors. In his description of the leaf anatomy of *P. vitiensis*, Bertrand makes the statement that there is one duct under the vein, and one duct on each side of this one in the middle of the parenchyma. In the accompanying figure of a transverse section of a leaf the lateral ducts are shown near the

leaf margins, occupying much the same position as the accessory resin canals in the leaves of *P. elongatus* and several other *Eupodocarpus* species. Bertrand's statement is endorsed by Feustal (8) and accepted by Florin, but van Tieghem (35), on the other hand, declared that he was unable to find in the leaf of *P. vitiensis* the secretory canals in the parenchyma described by Bertrand, and could only discover a single dorsal canal in the neighbourhood of the vascular bundle. The present writer, making use of a co-type of the species (Seemann No. 576), has likewise failed to discern any ducts in the mesophyll, only a single resin canal, lying below the vascular bundle, being visible in the leaf sections.

The number of resin canals in the leaves of *P. Rospiglosii* also remains in doubt. According to Florin, there are, in addition to two lateral canals in the mesophyll, three others beneath the vascular bundle, as in the leaves of *P. macrophyllus* (*Eupodocarpus*). In the material examined by the writer, three resin canals only can be seen in the leaf sections, instead of five as reported by Florin, and these are situated one under the vascular bundle, and one in the mesophyll on each side, near the leaf margin. An interesting commentary on these conflicting opinions is afforded by the description given by Mahlert (17) of the leaf anatomy of a *Podocarpus*, which he found, labelled *Polypodiopsis*, in the Leipzig Herbarium. Mahlert begins with a citation of Bertrand's figure of a leaf section of *P. vitiensis*, and after enumerating the principal anatomical features of the leaves of the Leipzig specimen, he proceeds to give particulars of the secretory system. According to him, there is one resin canal (sometimes divided to form three canals) under the phloem, and two in the mesophyll on each side, one of these being in the middle of each flank, the other being near the leaf margin. From these run short branches, so that he counted in a cross-section as many as four resin canals in each half of the leaf. The writer has in his possession a specimen of a *Podocarpus* which was growing at Kew under the name of *P. montanus*, but which is undoubtedly a *Polypodiopsis* species from the character of its foliage and the anatomy of its leaves. It has not been possible to obtain any information as to the origin of this plant beyond the fact that the seed from which it was raised came from the Herbarium at Kew many years ago. The reason for mentioning this plant at all, when its history is imperfectly known, is because its leaf anatomy agrees closely with that of the specimen described by Mahlert. In transverse sections of the leaves five resin canals are clearly visible, four of these being

situated in the mesophyll and one under the vascular bundle. The canals in the mesophyll occur in pairs, one each side of the vascular bundle, the innermost one of each pair lying midway between the bundle and the leaf margin, and the outermost canal being almost at the margin. This arrangement of the lateral resin canals is thus very similar to that in the leaves of the *Polypodiopsis* species described by Mahlert. There is, however, but one canal below the phloem in the Kew specimen, whereas, according to Mahlert, there are sometimes three canals under the vascular bundle in the leaves of the Leipzig specimen. The writer has been unable to discover in his specimen any indication of the branching of the canals mentioned by Mahlert.

It can only be assumed, from the divergent views expressed by the different observers on the secretory system in the leaves of these species, that the number and distribution of the resin canals is subject to variation, although the reason for this is not at present clear, and requires further investigation. Mahlert has stated that the number of canals may be increased by a process of branching, and the present writer, in another paper (21), has drawn attention to the occurrence of a similar phenomenon in the leaves of certain species of *Picea*. If this form of branching is sporadic, and not constant, this might account for the variable number of resin canals observed in the leaves of *Polypodiopsis* species. No such variation is found in the leaves of *P. minor*, however, there being only one resin canal below the vascular bundle in this species, and none at all in the mesophyll. On this point all authorities agree.

Apart from these apparent inconsistencies of the secretory system, the leaves of the species included here in *Polypodiopsis* are much alike in their general leaf anatomy, and can be distinguished individually only by minor differences in the disposition of certain tissues, or by the comparative size of the elements of which these are composed. In this way, as was explained in the context, the three species may be separated anatomically by the character of the hypodermis, which is slightly different in each one, or by the nature and distribution of the lignified cells, which occur in varying quantity in the mesophyll of the leaves. In the decussate arrangement of the foliage, and in the torsion of the leaves, as well as in the pattern of their leaf anatomy, except in regard to the number of resin canals, all three species bear a close resemblance to those of the second group in *Stachycarpus*.

NAGEIA Endl.

The *Nageia* section comprises seven species. These are *P. Blumei* Endl., *P. Fleuryi* Hickel,* *P. formosensis* Dümml., *P. Motleyi* (Parl.) Dümml., *P. Nagi* Makino, *P. nankoensis* Hayata, *P. Wallichianus* Presl, the New Caledonia species, *P. minor* Parl., with unicostate leaves, often included in this section, having been dealt with already under *Polypodiopsis* for reasons stated there. The *Nageia* species are mainly Asiatic: *P. Blumei* and *P. Motleyi* inhabit islands of the Malayan Archipelago, the former extending its range northwards to the Philippines: *P. Fleuryi* is a native of Annam; *P. formosensis* and *P. nankoensis* are Formosan, the latter being found also in Hainan; *P. Nagi* is distributed widely in China and Japan—it occurs also in Formosa; *P. Wallichianus* is an Indian species found throughout the monsoon region in Khasia, Assam, and Burma.

The foliage of the *Nageia* species is characteristic, the leaves being broad and many-veined, in contrast to the generally narrower and unicostate leaves of the *Eupodocarpus* species, and they are borne on the branches in opposite or sub-opposite pairs, an arrangement which is uncommon in the genus. A curious feature of the foliage is the twisting of the leaf petioles, which has the effect of reversing the orientation of the leaves on one side of the shoot, while bringing those on both sides to lie in the same plane. The leaves may be relatively short, as in *P. formosensis*, where they seldom exceed 4 cm. in length, or they may be comparatively long, up to 13 cm., and in some cases as much as 16 cm. in length, as in *P. Blumei* and *P. Wallichianus*.

The *Nageia* species are separable into two groups, as in *Stachycarpus*, but here the chief distinguishing feature is the presence or absence of a receptacle below the seed, and morphological differences of the foliage take second place from a taxonomic point of view. The species in which a receptacle is always developed are *P. Blumei*, *P. Motleyi*, and *P. Wallichianus*, and in each of these species the foliage is amphistomatous to a greater or less degree. The four remaining species, *P. Nagi*, *P. Fleuryi*, *P. nankoensis*, and *P. formosensis*, which form the second group, are totally devoid of a receptacle, and the leaves are invariably hypostomatous. That the presence or absence of a receptacle in the region of the seed should thus be linked with the presence or absence of stomata on

* The writer has seen no material of *P. Fleuryi*, which is akin to *P. Nagi*, and it is therefore not possible to describe its leaf anatomy here.

the upper surface of the leaves is a point of some interest, and it has been commented upon by Florin, but this combination of characters is probably without any real significance, since in *Stachycarpus*, the only other section of the genus in which a receptacle is never formed, only one half of the species have hypostomatous foliage.

The leaves of all the species in this section are naturally different anatomically from those of every other *Podocarpus* species, since the number of vascular bundles is increased from one to many, and there is a corresponding decrease in the amount of transfusion tissue present, this being reduced to a small number of tracheids flanking each bundle. Bernard (2) claims that this "centripetal xylem" may extend so far into the mesophyll as to unite neighbouring bundles, but the writer has been unable to confirm this statement in any of the leaf sections he has examined. Below the phloem of the larger bundles there is usually a single resin duct, the occurrence of which in this position, and not in the mesophyll between the bundles, as in *Agathis*, serves to distinguish anatomically the foliage of the *Nageia* Podocarps from that of the Malayan species of *Agathis*, with which the former is liable to be confused. In this connection it may be recalled that Florin has shown that it is possible to distinguish between the leaves of *Agathis alba* and those of *P. Blumei* by differences in the construction of the epidermal tissue.

The number of veins in the leaves of each of the *Nageia* species remains remarkably constant, but those species with the largest leaves have the veins more widely spaced. In the broad leaves of *P. Blumei* and *P. Wallichianus*, for example, the average number of veins per centimetre of the cross-section is 10, whereas in *P. formosensis*, *P. nankoensis*, *P. Nagi* and *P. Motleyi*, with relatively shorter and narrower leaves, the number varies from 17 to 19 per centimetre at the widest part of the lamina.

The epidermal tissues have been so fully described by Florin that nothing can be added to his admirable account. According to him, there is a marked uniformity in the structure of the stomatal apparatus and epidermis throughout this section, the species differing only in the number of stomatal lines on the leaves, and being separated but slightly by the varying degree of cutinisation of the outer and radial walls of the epidermal cells. In surface view the radial walls present an undulating outline, which is not an uncommon character of the epidermal tissue in Gymnosperm leaves.

A hypodermis is present on both sides of the leaves in all *Nageia* species, and in those which have stomata on the upper surface the

continuity of the hypodermis is interrupted above as well as below. The hypodermis is discontinuous on both sides therefore in *P. Blumei*, *P. Motleyi* and *P. Wallichianus*, but in the remainder of the species, in which the stomata are confined to the under-surface, the continuity of the upper hypodermis is maintained unbroken throughout. For the most part, the hypodermis consists of a single layer, though occasionally individual elements, representing a second layer, are to be seen, and at the margins of the leaf the hypodermis is usually two or three cells deep. The elements composing this tissue are fibriform, being elongated longitudinally in the direction of the long axis of the leaf, and in transverse section they appear angular in outline, with a small lumen and a moderately thick, often stratified wall. In the species with amphistomatic leaves the hypodermal fibres reach their greatest dimensions, those of *P. Blumei*, for example, being from $30\ \mu$ to $36\ \mu$ in diameter. In the species with hypostomatous leaves, on the other hand, the hypodermis is composed of smaller cells of more uniform dimensions, measuring from $18\ \mu$ to $24\ \mu$ in diameter.

Strengthening fibres are not confined entirely to the hypodermal layer in these *Nageia* species, but are found also in large numbers scattered through the mesophyll, very much as they occur in the leaves of Cycads such as *Dioon*. These fibres have enormously thick walls in which stratification is plainly visible, and in most cases the cell cavity is almost obliterated. Like the elements of the hypoderm, with which they may be in close contact, these fibres are elongated in a longitudinal direction, and, in *P. Motleyi* for example, they may reach a length of 1.5 mm. In transverse section the fibres are circular in outline, and they vary considerably in breadth according to the species. In *P. formosensis* and *P. Motleyi*, fibres of more than $100\ \mu$ in diameter are common, but in *P. Blumei* and *P. Nagi* they are uniformly smaller, seldom exceeding $75\ \mu$ in diameter, while those of *P. Wallichianus* are from $36\ \mu$ to $42\ \mu$ across.

The relation between the size of the fibres and the number present in the leaves of the various species presents a striking contrast, for in those species where the fibres reach their greatest dimensions the number of fibres in a given area is from two to three times as large as in the leaves of species characterised by more slender fibres. Thus, *P. formosensis* has an average of 184 fibres per square centimetre of leaf section, *P. Nagi* has approximately 90 in an area of equal size, and in *P. Wallichianus*, which possesses the smallest fibres, the corresponding number is 64.

The presence of so many supporting elements in the mesophyll of the *Nageia* species is almost without parallel in any other section of the genus, for, although similar elongated fibres are found intermixed with isodiametric sclereids in the leaves of certain *Stachycarpus* species, these are less widely dispersed and never occur in such quantity. In the comparatively narrow foliage of *Eupodocarpus* species sufficient rigidity would seem to be assured by the presence of the accessory transfusion tissue, and by the peculiar lignified elements of the mesophyll referred to earlier in this paper.

Palisade tissue is present in the leaves of all *Nageia* species, although in some cases, and in *P. Wallichianus* in particular, the amount is so small that it is practically negligible. It is always developed in some quantity beneath the upper epidermis in the species with hypostomatous leaves, but in those with amphistomatous leaves the differentiation of the palisade tissue is both unequal and irregular. This is particularly noticeable in the photosynthetic systems of *P. Blumei* and *P. Wallichianus*, which exhibit such contradictory features that the interpretation of their physiological anatomy presents rather a difficult problem.

It is generally stated that the leaves of the *Nageia* species, which are borne in two ranks on opposite sides of the shoots, are brought to lie in one plane by a twisting of the leaf stalks. In the species with hypostomatous foliage, the leaves on both sides of the shoots are so orientated that in every case it is the morphologically upper epidermis that is exposed to the incident light, and the leaves are structurally dorsiventral, with palisade tissue on the ventral side and spongy tissue on the dorsal side. The orientation of the vascular bundles is perfectly normal in the leaves of both ranks, the xylem forming the upper half of the bundle on the adaxial side, with the phloem beneath it on the lower side. This is the usual arrangement of the conducting tissues in normal leaves. In the species with amphistomatous foliage a very different condition is found, for here the leaves of one rank only remain normal as regards the orientation of their tissues, while those on the opposite side of the branch are so completely rotated on their axis that the morphologically under-surface becomes uppermost. In *P. Blumei* and *P. Wallichianus* this inversion of the lamina is accompanied by certain changes in the internal structure of the organ, but in *P. Motleyi*, for some reason, the arrangement of the non-vascular tissues in the rotated leaves remains unaltered. In direct contrast to the quasi-normal state of the foliage in the hypostomatous species, the leaves of which are uniformly bifacial, the normally

orientated leaves of all three amphistomatous species are definitely isobilateral, while those that are inversely orientated either remain isobilateral as in *P. Motleyi*, or become virtually bifacial as in *P. Blumei* and *P. Wallichianus*. The foliage of the former species is therefore composed of leaves which are all isobilateral in character, whereas that of the two latter species comprises two types of leaves, those on one side of the shoot being isobilateral, while those on the opposite side are bifacial.

Structurally, the isobilateral leaves of all three species are essentially alike, apart from such specific differences as have been previously described, and are characterised by a meagre development of palisade parenchyma under each epidermis, the stomata being more or less equally distributed over both surfaces. In *P. Motleyi*, the only recognisable distinction between the isobilateral leaves which show reversed orientation and those that do not is the inversion of the vascular bundles. In the bifacial leaves of *P. Blumei* and *P. Wallichianus*, on the other hand, the palisade parenchyma contiguous to the morphologically under epidermis, now exposed to light, by the reversion of the lamina, is increased in amount, forming a distinct palisade tissue, supposedly as a response to photic stimulation. As might be expected, the transposition of the epidermal tissues in these bifacial leaves has been followed by a redistribution of the stomata, there being a considerable reduction in their number on the morphologically under-surface, overlying the augmented palisade tissue, while, in the morphologically upper epidermis, now reversed in position, they are exceedingly numerous, and open into the intercellular spaces of a pseudo-spongy parenchyma. The hypodermis remains interrupted on both sides of the leaves where stomata occur, although the gaps are naturally less frequent over the palisade tissue. A statement by van Tieghem that the lower hypodermis in the leaves of *P. latifolia* (*P. Wallichianus*) is continuous is obviously incorrect. In the bifacial leaves of *P. Blumei* and *P. Wallichianus*, as in the inverted leaves of *P. Motleyi*, the reversed orientation of the vascular bundles is clearly visible, for the xylem is now directed downwards, and the phloem, with its associated resin duct, is contiguous to the palisade tissue on the adaxial side. This inversion of the vascular tissues is proof of the fact that the functional palisade tissue actually adjoins the morphologically under epidermis of the leaves.

The anomalous state of the foliage in *P. Blumei* and *P. Wallichianus* apparently misled van Tieghem (35), for he has described the leaves of *P. agathifolia* (*P. Blumei*) as having palisade tissue

on both sides, and those of *P. latifolia* (*P. Wallichianus*) as "lacuneuse en haut, palisadique en bas." This is only half the story, however, and it would appear that van Tieghem was unaware that the leaves on one side of the shoots in the species he named are structurally different from those on the opposite side. Bernard's figure (2) (fig. 20) of a cross-section of a leaf of *P. latifolia* forma *ternatensis* (*P. Blumei*) is similarly misleading, as it portrays a single layer of palisade parenchyma on the morphologically upper side and none on the under side.

The lack of uniformity in the photosynthetic system of the species with amphistomatous foliage is a morphological fact that is difficult to interpret on the ground of physiological expediency. Granting that the leaves, bilaterally arranged on the plagiotropous shoots, are all lying in one plane, due to the torsion of the petioles, then the angle of illumination should be the same for each leaf, whichever surface is presented to the incident light, and it seems reasonable to assume that the amount of palisade tissue developed on the side exposed to the light ought to be proportionately the same in the leaves on both sides of the shoots. But in *P. Blumei* and *P. Wallichianus* this is not the case, for it has been shown that in these species the leaves on one side of the shoots are characterised by a quantitative increase of the palisade tissue underlying the illuminated surface, while, in the isobilateral leaves of the opposite rank, the palisade parenchyma is as shallow on the exposed side as on the shaded side. It has been demonstrated by Haberlandt that the inception of the palisade tissue takes place in most cases while the leaf is lying in darkness within the bud, and relatively weak illumination is sufficient to start the series of developmental processes which culminate in the differentiation of the palisade tissue, while bright light leads to a quantitative increase of this tissue. If this is so, then it would appear, from the unequal differentiation of the mesophyll in the leaves of these two species, that one set of leaves has been subjected to a greater degree of illumination than the other set on the same branch, which is most unlikely if both sets of leaves lie in the same plane. Nor does it seem feasible that the photosynthetic tissue of the leaves on one side of the axis could be less malleable under the impact of photic stimulus than those on the opposite side. Nevertheless, the fact remains that the foliage of *P. Blumei* and *P. Wallichianus* is made up of two types of leaves, arranged in two rows on opposite sides of the plagiotropous shoots, those on the one side being virtually dorsiventral and adapted for vertical illumination, while those on the other side are essentially

isobilateral and have the appearance of being organised for the reception of light equally on both surfaces.

The problem is further complicated by the fact that in the foliage of *P. Motleyi* no such distinction exists between the leaves on either side of the plagiotropous shoots. All the leaves are isobilateral in character, whichever way the lamina is orientated. As it is highly improbable that the photosynthetic system of this species is less plastic than that of *P. Blumei* and *P. Wallichianus*, the absence of any adaptive modification of the leaf structure, such as that exhibited by the inversely orientated leaves of the latter species, suggests that none is necessary in this case. Yet, the phyllotaxy of the leaves and their orientation is practically identical in all three species, and if a quantitative increase of the palisade parenchyma is apparently not essential to the plant economy of *P. Motleyi*, what are the special circumstances which make an increase necessary in virtually half the foliage of *P. Blumei* and *P. Wallichianus*? This is a question to which no satisfactory answer can be given at the moment, and only the plant physiologist, with living material at his disposal, is likely to arrive at an adequate explanation of the physiological anatomy of the leaves of these three species.

The writer wishes to make it clear that the account of the leaf anatomy of *P. Motleyi* given in this paper is based on an examination of Beccari's specimen (No. 2649) from Sarawak, to which Parlatore (23) gave the name of *Podocarpus Beccari*. This explanation is necessary because the writer is not convinced of the validity of the species bearing Motley's name, which forms the basis of Dümmer's new combination (7). The history of this species is worth repeating here.

Prior to the discovery and recording of Beccari's *Podocarpus*, Parlatore (24) had described a sterile specimen, collected by Motley (No. 1300) in southern Borneo in 1857, under the name of *Dammara Motleyi*. About the same time Seemann (29) put forward the suggestion that Motley's plant might be a *Podocarpus*. This supposition was not accepted by Warburg (36) apparently, when, at a later date, he transferred *Dammara Motleyi* to the genus *Agathis*, retaining the specific name assigned to it by Parlatore. Some years later Seward and Ford (30), working on the Araucarieae, made an investigation of the leaf anatomy of Motley's specimen in the Kew Herbarium, in the hope of being able to establish its identity decisively by this means. The result of the examination is given in these words: "The lamina, which is almost isobilateral, is

characterised by the occurrence of resin canals between the vascular bundles, and by numerous thick-walled fibres, with hardly any lumen, below the epidermis. In this and other features the anatomy conforms to that of the leaves of *Podocarpus Nageia*." Was this intended to refer to *P. Nagi*, or to the *Nageia* section? In any case, the concluding statement is not in accordance with the facts, for it is well known that in *Podocarpus* the resin canals of the leaves are below and not between the vascular bundles, which is their position in *Agathis*. The thick-walled fibres below the epidermis, to which reference is made, are probably those forming the hypodermis, and no mention is made of the fibres scattered through the mesophyll which form such a characteristic feature of sections of *Podocarpus* leaves. Dümmer does not say whether or not he examined leaf sections of Motley's specimen; nevertheless, he evidently accepted the view that the plant in question is a *Podocarpus*, despite the statement that the resin canals in the leaf are situated between the vascular bundles. When quoting Seward and Ford's description of the leaf section, however, Dümmer inserted the word "below" in parenthesis, after the word "between," justifying this action by referring to a letter received from Seward in which the latter had stated that in *Podocarpus* the resin canals of the leaves are below, in those of *Agathis* between the veins. Whether Seward merely intended to correct the false impression given by his original statement on the characters of *Podocarpus* leaves, or was in fact admitting an error of observation in describing the position of the resin canals in Motley's specimen, is not clear.

In the brief summary which Dümmer gives of the characters of *P. Motleyi* (comb. nov.) he makes the significant assertion that the leaves have a very short, broad, not twisted petiolar base, whereas Parlatore had described the leaf base of Beccari's specimen as "angustatis et subcontortis" and that of Motley's plant as "attenuatis et vix contortis." Parlatore, himself, evidently did not think that the two specimens belonged to the same species. Unfortunately, the present writer has had no opportunity of examining Motley's specimen, but in view of the somewhat conflicting evidence adduced by Dümmer in support of the new combination, he cannot regard that author's identification of the specimen as being conclusive, and therefore he accepts the name of *P. Motleyi* with reservation.

From the foregoing account of the leaf morphology of the species in the *Nageia* section it will be evident that those with amphistomatous foliage are distinct from those with hypostomatous

leaves, not only because of the difference in the distribution of the stomata, but also by reason of the inconsistencies which mark the structure of the leaves of the former. In *P. Nagi*, *P. nankoensis*, *P. formosensis*, and probably in *P. Fleuryi* also, the leaves are, without exception, dorsiventral in character, and because of the absence of stomata from the upper surface, the hypodermis is continuous on that side, though interrupted opposite the stomata on the under side. In *P. Blumei*, *P. Wallichianus* and *P. Motleyi* the leaves are constitutionally isobilateral, although in the first two species mentioned they become in part bifacial by modification, but in this case, as in the isobilateral leaves, the hypodermis on both sides is always discontinuous. It becomes a comparatively simple matter, therefore, to determine to which group a *Nageia* species belongs by means of its leaf anatomy alone. It is not so easy, however, to identify the individual species of each group by the same method, because of the similarity of structure, especially noticeable in those with hypostomatous leaves, and it has been found that in most cases the only anatomical features that can be utilised for this purpose are those which are quantitatively different in each species. For example, in the description of the leaf anatomy of *P. formosensis* it was pointed out that the number of fibres present in a given area of leaf section is, on an average, more than double the number seen in a similar segment of a leaf of *P. Nagi*. Moreover, the fibres of *P. formosensis* are visibly larger in diameter than those of *P. Nagi*, and they often occur in groups of three or more together, whereas in the latter species they are almost always isolated. The difference in number and size of the fibres is so apparent in transverse sections of the leaves of these two species that there should be no difficulty in distinguishing between them. The leaves of *P. formosensis* are similarly distinct from those of *P. nankoensis*, which approximates more closely to *P. Nagi* in its leaf anatomy, although the fibres of the mesophyll are relatively thicker and are more numerous than in the last-named species (150 in a square centimetre). The hypodermal fibres are the same size in all three species.

From this analysis of their leaf anatomy it is seen that the leaves of these species conform to the same general pattern, differing so slightly in detail that the extent of the differences can only be computed on a numerical basis, when it becomes apparent that as regards their leaf anatomy the leaves of *P. nankoensis* are intermediate between those of *P. formosensis* and *P. Nagi*. It should be borne in mind that anatomical features, such as these fibres,

may differ in number and vary in size in different leaves, and it is necessary to examine as many leaves as possible in order to eliminate individual inequalities and obtain an average estimate of their frequency in any one species.

Among the species with amphistomatous foliage *P. Motleyi* is unique, since all its leaves are of the isobilateral type, while the fibres of the mesophyll are more numerous and have a greater diameter than those of either *P. Blumei* or *P. Wallichianus*. The leaves of *P. Motleyi* are much smaller than those of the other two species, but the veins are more closely set together, and in this respect it resembles *P. formosensis*, the leaves of which are normally only half the size of those of the other hypostomatous species. It has been shown that the fibres in the smaller leaves of *P. formosensis* are likewise greater in number and larger in diameter. *P. Blumei* and *P. Wallichianus* are readily recognisable by the diversity of structure in the paired leaves, the bifacial leaf of each pair being distinguishable from the leaves of *P. Nagi* and its allies by its amphistomatous character and the interrupted hypodermis. There are no outstanding differences, however, between the leaf anatomy of *P. Blumei* and that of *P. Wallichianus*, although the fibrous elements in the mesophyll of the former show a slight increase in number and size over those in the leaves of the latter species.

As it was pointed out in the context, the species of the *Nageia* section are separable into two groups on a point of difference in the morphology of the female strobilus, and each group is further characterised by the presence, or absence, of stomata on the exposed side of the leaves. It has been shown that the localisation of the stomata on one, or both, of the leaf surfaces is correlated with certain fundamental differences in the leaf anatomy, which are more striking even than those exhibited by the species of *Stachycarpus*. Moreover, the two groups into which the *Nageia* section is subdivided are not only morphologically distinct, but are also geographically separated. The group comprising *P. Blumei*, *P. Wallichianus* and *P. Motleyi*, with amphistomatous leaves and a receptacle below the seed, is widely spread from India through the Malayan Archipelago to the Philippines, the broad-leaved species, such as *P. Blumei*, being typical of the rain-forest flora. The group of species with hypostomatous foliage and without a receptacle, which includes *P. Nagi*, *P. formosensis*, *P. nankoensis* and *P. Fleuryi*, has a more northern distribution, ranging over parts of eastern China, Indo-China, southern Japan, and Formosa.

Taking all the points of difference between the two groups of

Nageia species into consideration, it would seem that their inclusion in the same section is scarcely in strict accord with taxonomic principles, and each group of species might well be raised to the status of a sub-section, or even to the rank of section in the genus.

EUPODOCARPUS Endl.

Eupodocarpus is by far the largest section of the genus, comprising over 50 species, and it is, geographically, the most widely spread, being represented in the ligneous floras of all but one of the great continental areas, as well as in those of many of the islands of the Pacific and the Malayan Archipelago. Of the individual species, *P. neriifolius* has the greatest range of distribution, being found in China, India, Sumatra, Java, Borneo, Celebes and New Guinea. Others, like *P. oleifolius*, are equally at home in widely separated localities, under dissimilar climatic conditions. Nevertheless, Eupodocarpus constitutes a natural assemblage of species, united by the special characters of the reproductive organs, which show little variation throughout the section, and by the similarity of the vegetative parts, particularly of the foliage. Male strobiles occur singly, or several together, in the axil of the leaves, or they may be aggregated to form a spicate inflorescence: the female reproductive organ is also axillary in position, and, as in the section Nageia, a fleshy receptacle is formed below the seed, often with two narrow bracts at its base. In their vegetative habit, the species of Eupodocarpus are either trees, sometimes of considerable height, or low-growing shrubs, densely branched or of straggling form. In the great majority of the species the leaves are spirally arranged, and, for the most part, are either linear or lanceolate in shape, varying considerably in length, however, according to the species. Sometimes the midrib of the leaf is prominent above as well as below, as in *P. neriifolius*, *P. Rumphii* and *P. Ledermannii*, and more rarely it is distinctly grooved on the upper surface, as in *P. coriaceus* var. *sulcatus*, *P. gnidioides*, *P. macrostachyus*, *P. nivalis*, *P. oleifolius* and *P. ulgurensis*. In every case the leaves are single-nerved, and the stomata are always confined to the lower surface in the adult state. In their general construction the leaves of all the species are much alike, although there are some notable exceptions, and in the disposition of the secretory system there is a certain amount of variation. This variation makes it possible to separate the species into groups, and since the groups are in the main geographically distinct, the arrangement of the resin canals appears to have some taxonomic significance.

Unlike those of the sections previously discussed, the species of *Eupodocarpus*, with very few exceptions, possess a well-defined accessory transfusion tissue in their leaves, and a hypodermis of some description is always present, giving additional support to the tissues. The exceptions referred to above, as being without a definite accessory transfusion tissue in their leaves, are *P. alpinus* indigenous in Tasmania, *P. acutifolius*, *P. nivalis*, *P. Totara*, *P. Hallii* all natives of New Zealand, *P. gnidioides* found only in New Caledonia, and *P. nubigenus* a South American species occurring in Chili and Patagonia. It is curious that such a varied assortment of species, from different geographical groups, should be linked together by this negative character. In the leaves of these species the narrow, elongated elements, typical of accessory transfusion tissue, are replaced by cells which are broad and short, resembling the cells of the mesophyll among which they lie, except that they are without living contents and have lignified walls with simple pits. These cells are essentially similar to the thick-walled elements found in the mesophyll of the leaves of *Stachycarpus* species, such as *P. Mannii* and *P. usambarensis*. It was to this form of element, in the leaves of *P. alpinus*, that Worsdell applied the term "relic," to indicate that such cells are merely a last vestige of an accessory transfusion tissue, now no longer required to give rigidity to leaves of so small a size. It does not follow, however, that the absence of an organised accessory transfusion tissue is always associated with a reduction in size of the leaf, as Worsdell suggested, for this tissue may be well developed in species, such as *P. brevifolius* for example, of which the leaves are no larger than those of *P. Totara*.

In order to facilitate description of the leaf anatomy of such a large number of species, as well as to emphasise the significance of certain features as evidence of specific relationship, it will be necessary to group the species according to their geographical distribution, and consider the special characteristics of each group separately. With this end in view, the section has been divided into four geographical groups of species: (a) African, (b) Asiatic, Malayan, Polynesian, (c) Australian, New Zealand, (d) American. The position of the Polynesian species in this scheme is open to argument, but the expediency of including them in the second group will be justified when their leaf characters are discussed. It should be borne in mind that this grouping of the species is based upon the assumption that certain anatomical characters, not of an adaptive nature, may be regarded as being expressive of the affinity of the

species in which they occur, and since the combination of these characters is different for each group, but is essentially the same in the majority of species in any one group, it is inferred that the species of each geographical region are interrelated. There are some notable exceptions among the species which do not fit into this scheme, and reference will be made to these when the group with which they are associated comes under discussion.

(a) The species in the first geographical group are *P. elongatus* (Ait.) L'Hér., *P. Henkelii* Stapf, *P. latifolius* (Thunb.) R. Br. (South Africa), *P. milanjanus* Rendle (Tropical Africa), and *P. madagascariensis* Baker (Madagascar). All are tree forms, with spirally arranged leaves, the maximum length of which is 6.5 cm. in *P. elongatus* and *P. latifolius*, 10 cm. in *P. milanjanus* and 15 cm. in *P. Henkelii* and *P. madagascariensis*. Only in the leaves of *P. elongatus* is the midrib conspicuous on the under side, and in none of these species is it ever prominent above. In every case the leaf structure is very similar, and the species are not readily separable on anatomical grounds. In one particular respect all the species agree, for in the leaves of each one there are always five resin canals, and this distinctive character separates the African species from those of every other geographical group in *Eupodocarpus*. The position occupied by these five resin ducts in a leaf is interesting, since it recalls the arrangement in the leaves of *P. Rospigliosii*, as described by Florin (9). In the case of the African species, three resin canals occur below the vascular bundle, and the two additional canals are situated in the mesophyll, one close to the margin on each side.

These species agree also in other aspects of their leaf anatomy. An accessory transfusion tissue is always present between the palisade and spongy tissues, and an unbroken layer of hypodermal fibres extends from margin to margin across the upper side of every leaf. A similar layer is formed over the lower side of the midrib, and fibres occur also between the lines of stomata. Only in the relative depth of the hypodermis, and in the size of the fibres of which it is composed, are differences perceptible among the species. At various points in the upper hypodermis little groups of fibres occur, protruding into the underlying palisade tissue. This happens in all the species to a greater or less degree, and in *P. madagascariensis* the projecting groups of fibres, which are larger and more numerous in this case, extend through the parenchyma almost to the transfusion tissue, forming a series of girders, which give additional support to the leaf. In this species, as in all the

other African representatives, numerous sclereids are to be seen in the leaves, adjoining the vascular bundle or dispersed through the mesophyll. These often appear to be wedged between the palisade cells, and are frequently of a peculiar shape, with heavily thickened walls pierced with simple pits. These sclereids, which are common to many species of *Eupodocarpus*, give strength and rigidity to the leaves, and this probably accounts for the fact that they are most conspicuous in the long leaves of *P. madagascariensis* and *P. miljanus*. Regarding the epidermal and photosynthetic tissues, there is little to be said, for these present no outstanding features worthy of note. The character of the epidermal tissue in *Eupodocarpus* as a whole has been fully described by Florin, who states that the stomatal apparatus remains constant in its structure throughout the section.

From this account of the leaf anatomy of the species in this group it will be seen that there are no pronounced differentiating characters by which the individual species can be separated anatomically. Such a marked uniformity of leaf structure, combined with the singular arrangement of the secretory system, can only be explained on the ground of the common origin of the species concerned, which is merely a restatement of the commonly held belief, based on other criteria, that the African species of *Eupodocarpus* constitute a natural alliance of closely related forms.

(b) The second geographical group covers a much wider area than the first group, and contains a larger number of species, occupying a great variety of habitats. Included in this group are *P. Forrestii* Craib & W. W. Sm. (China), *P. neriifolius* D. Don (India, China, Japan, Malaya), *P. macrophyllus* (Thunb.) D. Don (China, Japan), *P. Nakai* Hayata (Formosa), *P. Kawai* Hayata (Tonkin), *P. deflexus* Ridl. (Malay Penin.), *P. polystachyus* R.Br. (Sumatra, Java, Borneo, Philippines), *P. Teysmannii* Miq. (Sumatra, Borneo), *P. brevifolius* (Stapf) Foxw. (Borneo, Philippines),* *P. Koordersii* Pilg. (Java), *P. Brassii* Pilg., *P. Ledermannii* Pilg., *P. Schlechteri* Pilg., *P. thevetiifolius* Zipp. (New Guinea), *P. Rumphii* Blume (New Guinea, Celebes, Moluccas, Philippines), *P. Pilgeri* Foxw. (Celebes, Philippines), *P. costalis* Presl, *P. philippinensis* Foxw. (Philippines), *P. gnidioides* Carr., *P. longefoliolatus* Pilg., *P. novae-caledoniae* Vieill. (New Caledonia), *P. affinis* Seem. (Fiji).

As might be expected from its extended distribution, this group is less homogeneous in some respects than the previous one. Most

* *P. brevifolius* is recorded also from Hainan and Kwangsi by Metcalf (18) in "The Flora of Fukien," 1942.

of the species are tree forms, although some, such as *P. Forrestii*, are no more than shrubs. The foliage throughout is similar in shape but is variable in size, and in the juvenile state the leaves are frequently much longer than those of the adult tree. A few species are short-leaved, and of these *P. Brassii* has the smallest leaves, rarely exceeding 2 cm. in length, but in the majority of the species the leaves at maturity are comparatively long, those of *P. Rumphii* being as much as 25 cm. in length. In this connection it is interesting to note that, so far as it can be ascertained from the material examined, the amount of strengthening tissue present is not always in keeping with the size of the leaf. In several of the species in this group the midrib of the leaves is raised above the level of the rest of the upper surface, and this is particularly noticeable in the leaves of *P. affinis*, *P. costalis*, *P. Ledermannii*, *P. macrophyllus*, *P. neriifolius*, *P. Pilgeri*, *P. polystachyus*, *P. Rumphii* and *P. Schlechteri*. In the description of the leaf anatomy which follows, that of two of the species included in this group is of necessity omitted, no material of either *P. Kawaii* or *P. thevetiifolius* being available for examination.

In all the species belonging to the second group, with the exception of *P. gnidioides*, three resin canals are present in the leaves, and these are located beneath the phloem of the vascular bundle in every case. *P. gnidioides*, endemic in New Caledonia, differs from the rest of the species in having a single resin canal in its leaves, and in this respect it approximates more closely to the Australian and New Zealand species in the third geographical group. This bond of union is strengthened further by the non-development of an organised accessory transfusion tissue in the leaves of *P. gnidioides*, this tissue being absent also from the leaves of all *Eupodocarpus* species in New Zealand and one in Tasmania. Such similarity of features has a special significance when it is remembered that the species in question are placed together in one group by systematists, because they share the same character of the female reproductive organ, and in this respect they also show affinity with the American species of *Eupodocarpus*.

Another species which occupies an anomalous position is *P. elatus*, a native of Queensland and New South Wales. This species differs from its congeners in Australia in having three resin canals in its leaves, there being but one canal in the leaves of all other *Eupodocarpus* species in this region. Since the possession of three resin canals in the leaves has been taken as the character separating the species of the second geographical group from those of the Australian

group, *P. elatus* might have been included in the former group on this character alone. The significance of this lies in the fact that *P. elatus* has been recorded by Gibbs (11) as occurring in Fiji, and is said to have been found also in New Caledonia.

In the other anatomical features of their leaves, the species of this second group show less uniformity than do those of the preceding group, but the points of difference are not always sufficiently pronounced to make it possible to identify individual species by means of their leaf anatomy alone. The hypodermis, which is present in all the species on the upper side of the leaves and on the under side of the midrib, is discontinuous in the majority of cases, and occurs in unbroken sequence only in the leaves of *P. brevifolius*, *P. gnidioides*, *P. Koordersii*, *P. novae-caledoniae*, *P. philippinensis* and *P. Teysmannii*. In the leaves of these species the hypodermis consists mainly of a single layer of fibres, and is only occasionally double, generally in the midrib. In *P. gnidioides*, which, it has been pointed out already, differs in several respects from the species with which it is associated here, the hypodermal fibres are frequently superimposed one on another, and are so neatly packed together that they produce a characteristic mosaic appearance. In *P. brevifolius* the upper hypodermis is equally distinctive in transverse sections of the leaves, the elements composing it being alternately thick- and thin-walled. Except in *P. Koordersii* and *P. Teysmannii*, the fibres are comparatively large, although in several species those on the under side of the midrib are much smaller than those on the upper side. In the leaves of most of the species named above, isolated fibres also occur between the lines of stomata on the under side, but these have not been observed in this position in *P. brevifolius* or in *P. Koordersii*.

In the remainder of the species of this group the hypodermis is essentially discontinuous, and consists of fibrous elements which vary in size according to the species, and occur either singly or in short lines of two or more together, sometimes two or three cells deep. These fibres are uniformly small in the leaves of *P. Forrestii*, *P. macrophyllus* and *P. Nakai*, and are relatively large in the remaining species of the group. In *P. polystachyus*, in particular, the hypodermal fibres are conspicuous for their size, and present a distinctive appearance on account of the width of the lumen.

The manner in which the fibres are arranged to form the hypodermis is also characteristic of certain species, but, generally speaking, when the fibres are small, as in most of the Asiatic species, they form short rows, and when they are large they are generally

isolated in their occurrence, or they may be aggregated into small groups, as is the case in the leaves of *P. deflexus*, where the fibres encroach upon the palisade parenchyma in a manner reminiscent of the condition in the leaves of the African species of *Eupodocarpus*. Although the hypodermis is discontinuous, it should be noted that above and below the vascular bundle the layers are often unbroken, and it is only between the midrib and the margin on each side that the true character of the hypodermis is revealed. In the leaves of *P. Forrestii* and *P. macrophyllus*, however, the hypodermal tissue in the midrib appears to be consistently interrupted both above and below, while in *P. polystachyus* the gaps between the fibres occur only on the upper side, and in *P. Brassii* only on the under side of the midrib. Fibres are not uncommon between the stomata in the leaves of some species, chiefly those of Malaya and Polynesia, and have been observed in this position in *P. Ledermannii*, *P. Rumphii*, *P. Schlechteri*, *P. costalis* and *P. affinis*, but only occasionally in *P. Pilgeri* and *P. longefoliolatus*. The appearance of fibres in the stomatal region is a rare occurrence in the leaves of the Asiatic species, where practically the only hypodermal elements found on the abaxial side are those in the midrib and at the margin.

In addition to the accessory transfusion tissue, which is such a characteristic feature of the leaves of all the species, except *P. gnidioides*, sclereids are sometimes present in quantity in the palisade and spongy parenchyma. These sclereids, with their lignified walls, simple pits and wide lumen, are exact replicas, on a smaller scale, of the elements which take the place of accessory transfusion tissue in the leaves of species such as *P. alpinus* among others. In view of Worsdell's interpretation of their nature in this species, it is interesting to find these sclereids actually associated in many cases with the transfusion tissue which, in *P. alpinus*, they were said to replace.

In the group of species under discussion, sclereids have been seen in the leaves of *P. deflexus*, *P. Koordersii*, *P. Ledermannii*, *P. Rumphii*, *P. Schlechteri*, *P. novae-caledoniae*, *P. longefoliolatus* and *P. affinis*, but so far their presence has not been detected in the leaves of Philippine endemics, nor in several Malayan species in which they might be reasonably expected to occur. Fibrous elements, similar to those of the hypodermis, have been observed in the vicinity of the vascular bundle in the leaves of all the species of this group, with the exception of *P. gnidioides*.

Other features of the leaves, to which some reference must be

made, are the photosynthetic tissue and the cuticle, which are variable in amount in different species. The palisade tissue in the leaves of *P. macrophyllus* and *P. Forrestii*, for example, is relatively deep, and is in marked contrast to the extreme shallowness of the corresponding tissue in *P. neriifolius*. *P. Ledermannii*, *P. Koordersii* and *P. Rumphii* are also remarkable for the small amount of palisade parenchyma present in their leaves, a peculiarity which doubtless is of some ecological significance. In the leaves of *P. Brassii*, on the other hand, the palisade tissue is notably enlarged, and the cuticle is well developed here, as it is also in the leaves of *P. deflexus*, *P. gnidioides* and *P. novae-caledoniae* among others. It is worth noting also that in *P. Teysmannii*, according to Florin, exceptionally large crystals are to be seen along the radial walls of the epidermal cells. Many other instances might be given of the variability of these inconstant features, but the chief concern is with the specific characters which are capable of being utilised for identification purposes.

It has been pointed out already that all these species, with one exception, have three resin canals in their leaves, and the chief line of demarcation in the group is provided by the characters of the hypodermis. Among the species with a continuous hypodermis, *P. Koordersii* and *P. Teysmannii* are distinguishable from the remainder by the small size of the hypodermal fibres in their leaves, and are separable from each other by the presence of sclereids only in those of the former, as well as by the occurrence of fibres among the stomata in the leaves of the latter species. *P. gnidioides* is unique among the species of this group in being without accessory transfusion tissue in its leaves, and it is therefore readily distinguished from *P. brevifolius*, the only other short-leaved species with a continuous hypodermis. The extensive development of the accessory transfusion tissue in the long leaves of *P. philippinensis*, with consequent diminution of the parenchyma above and below it, is sufficient to separate this species from *P. novae-caledoniae*, in the shorter leaves of which the transfusion tissue is much narrower, and the palisade parenchyma is correspondingly much deeper. The presence of numerous sclereids in the mesophyll of the latter, and their absence from the leaves of the former species, affords confirmatory evidence of identity in each case.

Among the species with a discontinuous hypodermis, *P. macrophyllus* and *P. Forrestii* can be distinguished from *P. neriifolius* by their thicker leaves, with deeper palisade tissue, and especially by the smaller hypodermal fibres, which are also differently arranged.

Similar features of the leaves serve to distinguish *P. Nakai* from *P. neriifolius*, but there appears to be no constant anatomical characters separating *P. macrophyllus* from *P. Nakai*, to which it is related, or from the Japanese sub-species *P. maki* Sieb. The arrangement of the fibres in the hypodermis of the leaves of *P. deflexus*, and the characteristic appearance and size of these in *P. polystachyus*, are specific marks in each case, while the occurrence of sclereids in the mesophyll of the former species constitutes a point of difference between them. Incidentally, the leaves of *P. deflexus* are twice as long as those of *P. polystachyus*, but lack the prominent midrib of the latter. The New Guinea species, *P. Ledermannii*, *P. Rumphii* and *P. Schlechteri*, are all much alike in their leaf anatomy, as might be expected in view of their kinship, and there are no contrasting features by which they may be individually recognised. *P. Brassii*, which is associated with these species in New Guinea, is distinct, however, the leaves being much smaller, and there are neither sclereids in the mesophyll, nor fibres in the region of the stomata. Similarly, the absence of sclereids from the leaves of *P. costalis* and *P. Pilgeri* is a negative character which may be used to distinguish these Philippine species from *P. longefoliolatus* and *P. affinis*, in both of which sclereids are normally present in the leaves. In the latter species the hypodermal fibres dispersed among the stomata are much more numerous than those in a similar position in the leaves of *P. longefoliolatus*, where they are seen only occasionally. Nor is the accessory transfusion tissue in the latter species so well developed, or so clearly defined, as it is in *P. affinis*, a point of difference which is very noticeable in sections of the leaves. It is an interesting fact that the leaf anatomy of the three endemic species of New Caledonia, *P. gnidioides*, *P. longefoliolatus* and *P. novae-caledoniae*, should be so dissimilar that it is possible to identify each of them by this means alone. In the Fijian species, *P. affinis*, the leaves possess no special features indicative of the endemic nature of the species, and the sole peculiarity of the leaf anatomy is the unusual size of the two lateral resin ducts below the vascular bundle. From the Australian species, *P. elatus*, which is found also in Fiji, *P. affinis* can be distinguished anatomically by the discontinuous hypodermis of its leaves.

(c) The third group, comprising the *Eupodocarpus* species of Australia, New Zealand and Tasmania, may not be a natural one as regards the relationships of the component species, but it has the advantage of being a convenient arrangement from the point

of view of their geographical distribution. Included in this group are *P. dispermus* White (Queensland), *P. Drouynianus* Muell. (W. Australia), *P. elatus* R. Br. (New South Wales, Queensland, Fiji), *P. spinulosus* (Smith) R. Br. (E. Australia), *P. alpinus* R. Br. (Tasmania, Victoria), *P. acutifolius* Kirk, *P. nivalis* Hook. fil., *P. Totara* A. Cunn., *P. Hallii* Kirk (New Zealand).

The Australian species, on account of the bracteate character of the peduncle of the female strobile, are considered to be akin to the species in the preceding group, while those of New Zealand and Tasmania, in which there are no bracts below the female receptacle, approximate more closely to the American species of *Eupodocarpus*. The existence of two separate races in this antipodean group, postulated by the contrasting characters of the female reproductive parts, is borne out by a fundamental difference in the anatomical structure of the leaves, those of the Australian species possessing a typical accessory transfusion tissue, identical with that of the Malayan and most of the Polynesian species, whereas those of the New Zealand and Tasmanian species contain only the lignified elements with simple pits and wide lumen, dispersed in the mesophyll, the occurrence of which in these species, as well as in *P. gnidioides* and *P. nubigenus*, has been commented upon already.

With the exception of *P. elatus*, mentioned before, all the species in this group have one resin canal only in their leaves, and this is situated in the median line below the vascular bundle. In this respect the New Zealand and Tasmanian species resemble their *Eupodocarpus* congeners in America, with which they have other features in common. The Australian species, on the other hand, are divided on this point, *P. Drouynianus* and *P. spinulosus* having one resin canal in their leaves, while *P. elatus* has invariably three ducts below the vascular bundle. As the writer has seen no specimens of *P. dispermus*, which is said to differ from *P. elatus* in its longer leaves and seeds, and in the red colour of the receptacle, it is not possible to describe its leaf anatomy here, or to say how many resin canals are present in its leaves.

In view of the affinity of the Australian species to those of the Malayan and Polynesian group, as expressed by the similarity of the female strobiles, it is somewhat disconcerting to find that two of the former species should differ from the latter in having less than the customary number of resin canals in their leaves. What the exact significance of this discrepancy may be it is hard to say. The position of *P. elatus*, with three canals in its leaves, presents no difficulty, and its occurrence in the islands of Polynesia is

evidence of a close connection with the species of the preceding group. A statement made by Stiles, that the structure of the leaves of *P. elatus* and *P. polystachyus* seems to be essentially similar, is not, however, strictly correct, since there is a pronounced difference in the size and disposition of the hypodermal fibres in each case, which, it is unlikely, could be determined entirely by external conditions as Stiles (33) has suggested.

Apart from the discrepancy in the number of resin canals, a marked dissimilarity is evident in other features of the leaf anatomy of the three Australian species (*P. dispersus* is excluded). In *P. Drouynianus* and *P. spinulosus* the hypodermis on the upper side of the leaves, between the midrib and the margins, is interrupted at several points, more so in the latter than in the former species, but it remains continuous across the midrib on both sides. The fibres composing it are large and distinct, and occasionally are superimposed, but none is visible in the region of the stomata. In both species there is also a patch of fibres between the phloem and the resin canal, but in neither case is there any trace of sclereids in the mesophyll. There is quite a perceptible difference in the amount of cuticle developed on the leaves of these two species, that of *P. Drouynianus* being so thick that the epidermal cells appear dwarfed by comparison.

In their general leaf anatomy *P. Drouynianus* and *P. spinulosus* are much alike, and practically the only point of difference sufficiently obvious to be of use, apart from the cuticle, is that provided by the outline of the midrib as seen in sections of their leaves. In the former species the midrib is flat above and prominent below, while in the latter species it is slightly convex on both surfaces. In the much broader leaves of *P. elatus*, however, the internal structure is entirely different. The hypodermal tissue is continuous from margin to margin on the upper side, as well as on the under side of the midrib, and there are also rows of fibres between the lines of stomata. Sclereids are present in the mesophyll, and these are also found, intermixed with isolated fibres, in the parenchyma of the midrib. With leaves so different anatomically, it is a simple matter, by means of these alone, to distinguish between *P. elatus* and the two former species.

Among the New Zealand and Tasmanian species only *P. Totara* and *P. Hallii* are tree forms, the remainder being shrubs or bushes, sometimes of a straggling habit, as is the case in *P. nivalis*, and all have small leaves, rarely exceeding 2 cm. in length in the adult state. Anatomically, the leaves of all the species are very similar,

and are characterised by the sporadic development in the mesophyll of the large, thick-walled, pitted cells, to which frequent references have been made. A hypodermis is always present, and only in the leaves of *P. alpinus* and *P. nivalis* is its continuity interrupted, here and there, by the interposition of one or two non-fibrous elements. This condition is often more apparent in the leaves of cultivated specimens. Hypodermal fibres form a layer on the lower side of the midrib, and occur also among the stomata in all species, but are more numerous in the latter position in the leaves of *P. Totara* and *P. Hallii*. Apart from those forming the hypodermis, true fibres have not been observed elsewhere in the parenchymatous tissue of the leaves, but thick-walled cells surround the resin canal in *P. Totara*, and may be seen forming an arc above the xylem in the leaves of this and other species. The single resin canal, which is typical of all the species in this group, is variable in size and is noticeably large in *P. alpinus*, *P. nivalis*, and sometimes in *P. Hallii*, but it would be unsafe to regard this as a consistent feature in the leaves of these species. The similarity of the leaf structure in the two former species makes it almost impossible to distinguish between them anatomically, although, outwardly, the leaves of *P. nivalis* differ from those of *P. alpinus* in having a sulcate midrib. The groove is not always apparent, however, in plants in cultivation. Both species have stout and narrow leaves, and in transverse sections these present an appearance quite different from those of *P. acutifolius*, which are thinner. In the latter the hypodermis is scarcely ever interrupted, the sclereids are more plentiful, and the resin canal is comparatively small. In these respects the leaves of *P. acutifolius* approximate more nearly to those of *P. Totara*, except that the fibres in the region of the stomata in the latter species are distinctly more numerous.

Regarding *P. Totara* and *P. Hallii*, it has been stated by Cockayne (6) that these two species are distinguished only by the thick bark of the former and the thin papery bark of the latter, while the leaves—even those of the juvenile forms—are useless in diagnosis. The close relationship which is known to exist between *P. Totara* and *P. Hallii* is reflected in their leaf anatomy, this differing only in a few minor respects, such as the relative size of the resin canal and the variable amount of thick-walled tissue in the mesophyll. The latter may be developed to such an extent that Griffin (13) was led to describe it as an accessory transfusion tissue, which is a misnomer, for clearly it is not homologous with true accessory transfusion tissue, but would seem to have originated from the

elements of the mesophyll, and to have as its function the strengthening of the tissues of the leaf.

Some taxonomists consider *P. Hallii* to be merely a variety of *P. Totara*, and whether or not it should be accorded specific rank is still in doubt. Some years ago Briggs (4) approached the question of the status of *P. Hallii* from a new angle, when he investigated the chemical properties of the essential oil found in the leaves of this species, and demonstrated the presence of the hydrocarbon, phyllocladene. His view of the significance of this discovery is best expressed in his own words. He writes, "The isolation of phyllocladene from *P. Hallii* is therefore the first record of this diterpene in a species of *Podocarpus*, and since it differs from rimuene, obtained from *P. Totara*, it would appear from chemical evidence at least that *P. Hallii* should be given the status of a separate species."

A study of the New Zealand Podocarpaceae, whether made from a taxonomic or from a morphological standpoint, is rendered more difficult by the frequency with which hybridity may occur among the species. Cockayne (6) affirms that wild hybridism occurs on a vast scale in the New Zealand flora, and he has enumerated several hybrid groups among the taxads alone. One of these represents *P. Totara* $\times$ *P. Hallii*, and Cockayne has expressed the view that certain trees with leaves differing greatly in size and apices, which are met with in nature and in cultivation, may be compounded of these two species. This may explain the variableness which the writer has observed in the leaf anatomy of some cultivated specimens bearing either specific name, for it is possible that these are really heterozygotes, and the nonconformity to type of the leaf structure may be due to their genetical instability.

That certain features of the leaf anatomy are of some value in indicating specific relationships is clearly demonstrable in the case of the *Eupodocarpus* species of New Zealand, for it has been shown that the species in question agree closely with certain of their congeners in Tasmania, New Caledonia and southern Chile, not only in the characters of their reproductive parts, but also in the possession of a special type of leaf structure, which is peculiar to all of them, and, notwithstanding their present geographical isolation, is a mark of their common lineage. On this point a statement made by Forbes (10) in the course of a discussion on problems connected with the New Zealand flora is singularly appropriate and is worth quoting. He writes, "The typical northern forms are closely related to those found in Fiji, or even Malay, while side by side are

found species which are first cousins to those from Tasmania and Tierra del Fuego. Probably no other country exhibits such an extraordinary admixture, and the comparatively few conifers occurring amongst a multitude of broad-leaved species are drawn from the same wide area."

(d) The fourth and last group to be considered consists of the Eupodocarpus species which are indigenous to Central and South America and the West Indies. These are *P. guatemalensis* Standl. (Guatemala, Honduras), *P. pinetorum* Bartl. (Honduras), *P. Allenii* Standl. (Panama), *P. macrostachyus* Parl. (Costa Rica, Colombia, Venezuela), *P. oleifolius* D. Don (Costa Rica, Ecuador, Peru, Bolivia), *P. Purdieanus* Hook., *P. Urbanii* Pilg. (Jamaica), *P. coriaceus* Rich. (Jamaica, Colombia, Venezuela), *P. Ekmanii* Urb. (Cuba), *P. angustifolius* Griseb. (Cuba, Bolivia), *P. Buchii* Urb. (Haiti, Santo Domingo), *P. Roraimae* Pilg. (Guiana), *P. Lambertii* Klotzsch, *P. Sellowii* Klotzsch (S. Brazil), *P. glomeratus* D. Don (Ecuador, Peru), *P. Parlatorei* Pilg. (Bolivia, N. Argentina), *P. nubigenus* Lindl., *P. salignus* D. Don (Chile). It has been possible to secure authentic material of the majority of the species enumerated above, but, unfortunately, no specimens were available of *P. Allenii*, *P. pinetorum*, *P. Buchii*, *P. Ekmanii* nor *P. Roraimae*, and descriptions of their leaves are therefore not included in the account of the leaf anatomy of the American species. It is said that *P. Allenii* is closely related to *P. guatemalensis* and *P. pinetorum* to *P. oleifolius*. *P. Buchii* resembles *P. angustifolius* var. *Wrightii*, while *P. Ekmanii* approximates most nearly to *P. Urbanii*. *P. Roraimae*, according to Pilger who described this species, is allied to both *P. macrostachyus* and *P. oleifolius*.

The leaves of the species examined vary in length from 2-3 cm. in *P. Urbanii* to a maximum of 15 cm. in *P. guatemalensis*. The midrib is prominent above in *P. guatemalensis* and *P. angustifolius*, and is grooved in *P. Purdieanus*, *P. oleifolius*, *P. macrostachyus* and *P. coriaceus* var. *sulcatus*, a variety found in Guadeloupe.

The general pattern of the leaf anatomy is very similar throughout this group, although there is some slight variation of the structural details in a few species. In the leaves of all the species there is a single resin canal below the vascular bundle, and, except in *P. nubigenus*, an accessory transfusion tissue is always present in the mesophyll. A hypodermis is a universal feature of the leaves, and in all but *P. Parlatorei* and *P. salignus*, two notable exceptions, this tissue forms a continuous layer beneath the upper epidermis and across the lower side of the midrib. Hypodermal fibres are

also prominent among the stomata in the leaves of every one of the species examined. The fibres are frequently superimposed upon each other at different points, and where this happens the lowermost fibres are often the larger. There is also an appreciable difference in the size of the fibres, those in the leaves of *P. guatemalensis*, *P. macrostachyus*, *P. oleifolius*, *P. Lambertii* and *P. Parlatoarei* being generally smaller than those in the other species.

It was mentioned above that the hypodermal tissue is interrupted in the leaves of *P. Parlatoarei* and *P. salignus*, which is an unusual feature among the American species. The lack of continuity is more apparent in the former than in the latter species, where the gaps are few and far between, and it is equally characteristic of both cultivated and native plants.

Other fibrous elements, similar to those of the hypodermis, are to be seen in the parenchyma above and below the vascular bundle in the leaves of almost all the species, but they are generally few in number, except in *P. angustifolius* where they form a compact group contiguous to the xylem. Typical sclereids, with a wide lumen and simple pits in their walls, are of rare occurrence among the species of this group and have been observed in *P. oleifolius* and *P. nubigenus* only, although certain small, lignified cells of a circular shape, located in the tissue of the midrib of the leaves of *P. Purdieanus*, might be said to belong to this category. In *P. oleifolius* the sclereids are situated mainly in the palisade tissue, and are readily identified by their lignified walls and lack of contents. It is curious that this should be the only American species amongst those examined, in which sclereids are developed in the leaves together with accessory transfusion tissue. *P. nubigenus* is entirely different in this respect, for the leaves of this species contain no accessory transfusion tissue, and the formation of sclereids in the mesophyll is here analogous to the development of a sclerotic tissue in the leaves of the *Eupodocarpus* species of New Zealand. The sclereids of *P. nubigenus* have stratified walls, which are more strongly lignified than is the case in the corresponding elements in the leaves of the New Zealand species, but, taken in conjunction with the absence of accessory transfusion tissue, and the similarity of the female strobilus, the occurrence of these sclereids here has a special significance, since everything points to the existence of a close connection between this Chilean species and its congeners in New Zealand.

A peculiar feature of the accessory transfusion tissue in the leaves of certain other American species is worthy of note. In several

cases the walls of the transfusion tracheids are much thicker than is usual, while the elements themselves seem to be both shorter and wider, and are less regularly arranged. This condition is best seen in the leaves of *P. glomeratus*, and it is also evident, but to a less degree, in those of *P. angustifolius* and *P. Parlatoresi*. The epidermal tissue presents no special features in any of the species examined, and no diagnostic importance is attached to it. In some cases, of which perhaps *P. macrostachyus* is the best example, cutinisation of the lateral walls of the epidermal cells takes place to such a degree that the lumen of each cell becomes dome-shaped, and a characteristic effect is produced in the epidermis as a whole. This form of cutinisation is a common feature of epidermal tissues in general, but owing to a tendency to fluctuate, it is of little value for identification purposes.

It will be evident from this brief account of their leaf anatomy that the American species of *Eupodocarpus*, with the exception of *P. nubigenus*, are anatomically much alike, and only in a few cases are structural differences so sufficiently pronounced that these can be utilised to separate species. Thus *P. Parlatoresi* and *P. salignus* may be singled out by the lack of continuity in the hypodermis of their leaves, and *P. oleifolius* can be distinguished by the sclereids present in the mesophyll. The peculiar features of the accessory transfusion tissue in the leaves of *P. glomeratus* is another case in point, although it is possible that this species may be confused with *P. angustifolius*, except that in the latter the midrib is more prominent above. The size of the hypodermal fibres is an important point in certain cases, and may provide a clue to the identity of such species as *P. Lambertii*. But in other American species the anatomical characters alone are not sufficient to provide conclusive evidence of identity, and it will be necessary to take the configuration of the midrib in transverse section into account. In this way *P. guatemalensis*, with a protuberant midrib, may be distinguished from *P. macrostachyus*, the midrib of which is deeply grooved. In the leaves of *P. Purdieanus*, on the other hand, the midrib is prominent above as well as sulcate.

The homogeneous character of the leaf anatomy in the great majority of the *Eupodocarpus* species of America is somewhat surprising in view of their scattered distribution, and would seem to imply a close degree of affinity. At the same time they agree with the New Zealand species in the bractless state of the female strobile, and it is rather remarkable that, with one exception, they should not be in complete agreement also as regards their leaf

anatomy. It has been pointed out before that among the *Eupodocarpus* species in America *P. nubigenus* is exceptional in this respect, and, while all the other members of this group differ in possessing accessory transfusion tissue, this species alone resembles its allies in New Zealand in being without this tissue in its leaves. If certain anatomical features are inherent in the specific constitution, they are *ipso facto* of the nature of racial characters, in a restricted sense, and as such are indicative of the pedigree of the species. This being so, it follows that *P. nubigenus*, because of the distinctive features of its leaf anatomy, is more closely related to the *Eupodocarpus* species of New Zealand than are its congeners in America, which are characterised by quite a different type of leaf structure. It will be recalled that a parallel case exists in the section *Stachycarpus*, where the similarity of structure of the leaves of *P. andinus*, also a native of southern Chile, and those of the New Zealand species, *P. ferrugineus*, is a mark of their affinity.

The chief object of this study of the leaf anatomy of various species of *Podocarpus* has been to explore the possibility of utilising the anatomical features of the foliage as aids to the identification of the species. To accomplish satisfactorily a research of this nature, a large supply of material, from every type of habitat, is almost an essential requisite in order that the positive value of the characters employed for diagnostic purposes may be thoroughly tested. Such an ideal treatment of the subject is unfortunately impossible of attainment, and the descriptions of the leaf anatomy which are given in this paper are of necessity based upon a limited number of specimens, many of which, however, represent the types, or co-types, of the species examined. Despite restricted material, it is believed that the facts disclosed are of sufficient consequence to justify the undertaking, and, although it has been found impossible to establish the identity of every species by means of its leaf anatomy alone, the critical examination of leaf sections, with this end in view, has brought to light several interesting features hitherto overlooked: the irregularities of the photosynthetic tissue in the leaves of two species of *Nageia* is a case in point.

Practical experience has shown, however, that in the majority of the species examined, the leaf anatomy does present some special features which are peculiar to individual species, or to groups of allied species, and these, because of their stability, are of use as specific criteria, serving to distinguish the species possessing them from their congeners in the same or other geographical areas. Thus, when the foliage of different species is similar in external

appearance, as is often the case, the internal structure of the leaves may prove to be a deciding factor in identification.

Two classic examples of mistaken identity may be cited here as illustrations of the necessity of making anatomical investigation in doubtful cases, where external characters alone are insufficient to provide conclusive evidence of identity. The examples referred to are those of *P. celebica* Hemsl. and *P. palembanicus* Miq., both of which were described from sterile material, and in both cases external appearances proved to be deceptive, for the former is now known from its leaf anatomy to be a species of *Taxus*, while the latter has been shown to be an angiosperm.

Other cases, where the structure of the leaves is essentially the same in different species as it is in the African species of *Stachycarpus* and *Eupodocarpus*, are equally of interest to the taxonomist, for such marked conformity to type in the details of their leaf anatomy can only be interpreted as evidence of the close affinity of the species concerned. But, since the species in question have such an extended range of distribution through temperate and tropical Africa, and are exposed to varying climatic conditions, it is surprising that the anatomical features of their leaves should show so little evidence of modification in response to the influence of ecological factors operating in different environments. This is but another of the several problems arising out of this investigation of the leaf anatomy of *Podocarpus* species.

In conclusion, the writer would emphasise again the importance, stressed by him in a previous paper (22), of correctly assessing the potential value of structural features as specific indicators under all conditions, since the systematic significance of such features is determined by their degree of stability, as well as by the incidence of their occurrence in the species of a genus.

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EXPLANATION OF PLATES I-II.

Fig. 1.—*P. Blumei* (Elmer 1236). T.S. leaf, from one side of a plagiotropous shoot, showing feeble development of palisade parenchyma on both sides. $\times 50$.

Fig. 2.—*P. Blumei* (Elmer 1236). T.S. leaf with reversed orientation, from opposite side of plagiotropous shoot, showing development of palisade tissue on morphologically under side. $\times 50$.

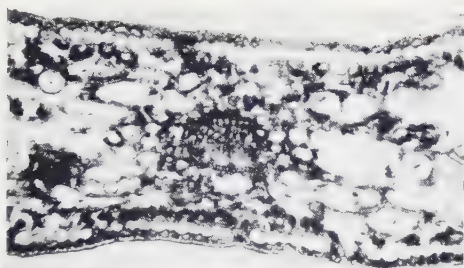
Fig. 3.—*P. Dawei* (Dawe 961). T.S. leaf, showing characteristic development of fibres above and below the vascular bundle, and lateral extension of transfusion tissue. $\times 95$.

Fig. 4.—*P. minor* (Schlechter 15331). T.S. leaf, showing similar development of fibres and extension of transfusion tissue. $\times 50$.

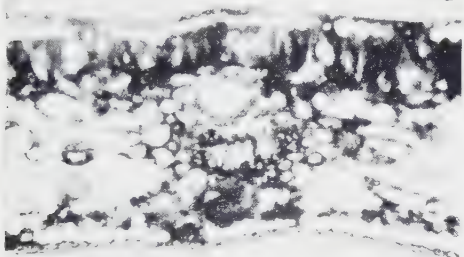
Fig. 5.—*P. ferruginoides* (Compton 1073). T.S. leaf, showing multiradiate idioblasts in the mesophyll. $\times 95$.

Fig. 6.—*P. gnidioides* (Schlechter 15329). T.S. leaf, showing sclereids in the mesophyll. $\times 95$.

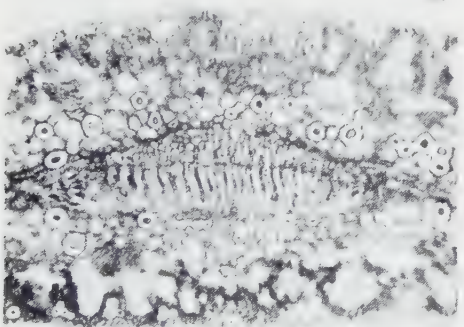
Fig. 7.—*P. madagascariensis* (Baron 3129). T.S. leaf, showing a single sclereid above the accessory transfusion tissue, contiguous to the fibres of the upper hypodermis. $\times 230$.



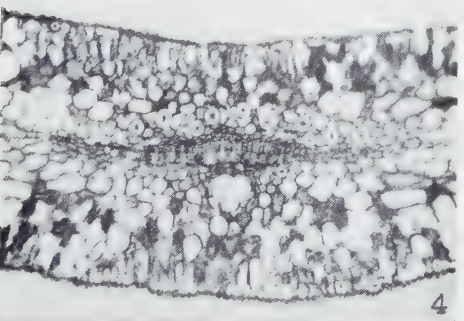
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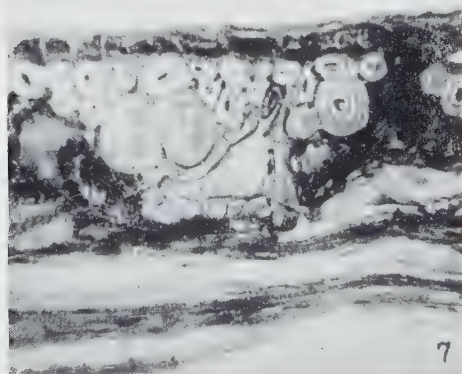
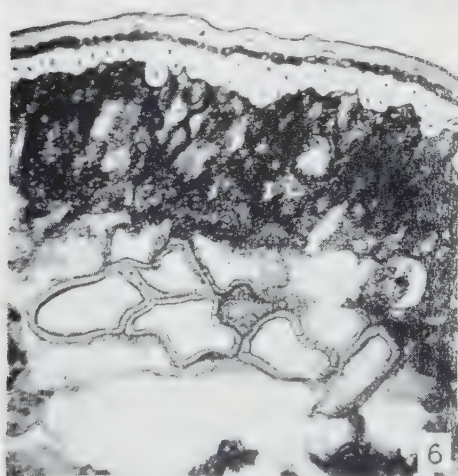
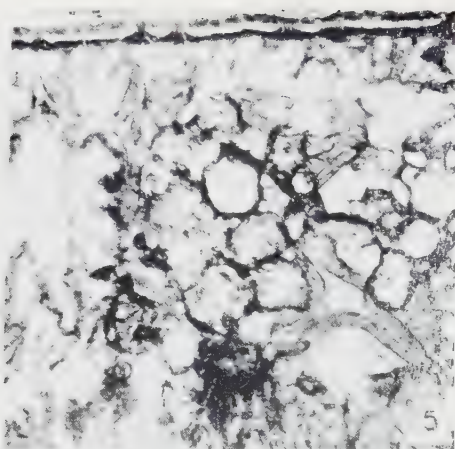
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THE GENUS PRIMULA: SECTION CORTUSOIDES Balf. f.

By W. WRIGHT SMITH and H. R. FLETCHER.

(Read 18th May 1944.)

The use of the name *Cortusoides* for a section of the genus *Primula* dates from the Third *Primula* Conference held in 1913. In his paper dealing with the Chinese species of *Primula*, read at that Conference, Balfour (1) treated Pax's section *Sinenses* as an aggregate and considered it convenient, at least in relation to horticulture, to divide its content into smaller groups which in his view were phyletic sections. Of these he enumerated eight, to each of which he accorded a brief description with citation of the species to be included. That such a division was to some extent practicable had occurred long before to Pax (2) in 1889 when he constituted the section *Sinenses*. He then indicated that his section contained at least three very definite groups—one occupied by *P. sinensis*, a second, "*Poculiformia*," embracing *P. obconica* and its allies, and a third, "*Cortusina*," containing *P. cortusoides* with six other species. A fourth is hinted at in his reference to *P. malvacea*. It was also evident to him that the characters likely to be serviceable for such subdivision would be those of the calyx—its shape and whether it becomes accrescent in the fruiting stage or not. This emphasis on the calyx and subordination of the leaf-characters are exemplified in the key which he gives to the species (*l.c.*, 166). However, Balfour's tentative substitution of eight small sections to replace *Sinenses* perhaps carried subdivision rather too far. After all sectional value is a matter of opinion and does not necessarily argue any profound difference in the views taken of the species concerned. Subsequently in the review of the sections of *Primula* by Smith and Forrest (3) a middle course was taken and three sections outlined by Balfour—*Cortusoides*, *Mollis*, and *Geranioides*—were combined under *Cortusoides* Balf. f. Experience in the assessment of the species included in the section thus constituted supports their line of action. The cytological evidence afforded by the investigations of Bruun (4) advocates no marked divergence from the views previously expressed and may be said to give approval in turn, first to the soundness of the broad treatment by Pax, then to the validity of the fine distinctions in Balfour's

analysis, and finally to the sectional treatment of *Cortusoides* by Smith and Forrest with the proviso (Bruun, *l.c.*, 28) that the section could well be represented as composed of five subsections.

If therefore the correct policy is the breaking up of the Paxian aggregate, the section *Cortusoides* must be contrasted with the following allied sections—*Sinenses*, *Obconica*, *Malvacea*, *Pycnoloba*, and the adjacent *Reinii*. As all these except the last were within the major unit, they will necessarily have many features in common. The members of these sections lack farina but are generally well furnished with multicellular hairs; the leaves are revolute, very distinctly petiolate and are more or less lobed or have at least a tendency to lobing if only marginal; the flowers are never sessile nor the bracts saccate; the corollas are more or less infundibular, never campanulate. Thus the distinctions between the six sections are necessarily narrow and depend, as has already been hinted, on the structure of the calyx. The calyx in *Cortusoides* is more or less tubular or cylindric, usually rigid in texture, often furnished with many prominent ribs but shows little or no tendency to enlargement in the fruiting stage; the calyx teeth are erect and not patent, while the shortly oblong capsule is more or less included. The only marked exceptions to these generalisations are *P. Sieboldii* where the calyx is accrescent and the lobes somewhat patent and *P. Pauliana* where the capsule is extruded. From *Cortusoides* the kindred sections can now be distinguished as follows: *Sinenses* by the much inflated calyx which is widest at the base; *Pycnoloba* by the fantastically large calyx which quite dwarfs the corolla; *Malvacea* by the numerous superposed whorls or even racemes in the inflorescence as well as by the cupular foliaceous accrescent calyx with patent lobes exposing the fruit; *Obconica* by the cupular or campanulate-poculiform foliaceous calyx with broad lobes; *Reinii*, a small section confined to Japan, has much exserted capsules but is otherwise very closely akin and its separation from *Cortusoides* may not be wholly justifiable.

In this review the section is divided into two subsections—*Eu-Cortusoides* and *Geranioides*. The distinctions between them are not of much weight, but are serviceable for the purpose of a key and have at least the merit of not dissociating species which are undoubtedly akin. With the exception of *P. cortusoides*, which penetrates from Siberia to the west of the Urals to Ufa in European Russia, the section is wholly Asiatic, as are the allied sections. Its area extends throughout Siberia to Korea and Japan, from Central Asia to the northern and western provinces of China, to

the Eastern Himalaya and the adjoining parts of Tibet, and to just within the boundaries of N.W. Burma (in the case of *P. mollis*). The majority of the species have been at one time and another in cultivation in European gardens and several may be considered as established.

REFERENCES.

- (1) BALFOUR in Journ. Roy. Hort. Soc. London, xxxix, 139 (1913).
- (2) PAX in Engler's Bot. Jahrb., x, 164-166 (1889).
- (3) SMITH and FORREST in Notes Roy. Bot. Gard. Edin., xvi, 19 (1928), and in Journ. Roy. Hort. Soc. London, liv, 16 (1929).
- (4) BRUUN in Cytological Studies in Primula, 21, 125 (1932).

KEY TO THE SPECIES.

- A. Lateral nerves pinnately arranged; calyx with many nerves: Subsection
 B. Leaves $\pm$ orbicular, as long as broad, or only a little longer than broad: Eu-Cortusoides
 C. Leaves scarcely lobed, only slightly cut at the margin (West China and E. Himalaya):
 D. Leaves dentate-lobulate, glabrescent; calyx glabrous *violaris*
 DD. Leaves sinuate-crenate, usually very hairy; calyx $\pm$ pilose:
 E. Corolla monomorphic; calyx 10-12 mm. long, with broad base *mollis*
 EE. Corolla heteromorphic; calyx 5-9 mm. long, with narrow base *cinerascens*
 CC. Leaves lobed to $\frac{1}{3}$ or $\frac{1}{4}$, and so deeply lobed:
 D. Calyx glabrous (Central Asia):
 E. Corolla usually white; leaves sharply dentate *lactiflora*
 EE. Corolla usually $\pm$ purple; leaves bluntly dentate *Kaufmanniana*
 DD. Calyx pilose (West China) *polyneura*
 BB. Leaves ovate to oblong, up to twice as long as broad:
 C. Calyx non-acrescent, lobes erect:
 D. Pedicels less than 1 cm. long (W. Asia) *cortusoides*
 DD. Pedicels usually 1-3 cm. long, up to 5 cm. long (N.E. Asia)
 CC. Calyx accrescent, lobes patent (Japan, N.E. Asia) *saxatilis*
 Sieboldii
 AA. Lateral nerves mostly basal; calyx usually with few nerves: Subsection
 B. Flowers rose to purple; inflorescence umbellate: Geranioides
 C. Petiole with broad vagina at base; lamina glabrous below:
 D. Umbel very compact, sometimes almost simulating a capitulum *Normaniana*
 DD. Umbel lax:
 E. Scape usually 2-flowered (1-3 flowered), generally no longer than the leaves; corolla-limb 10-18 mm. diam. (S.E. Tibet, Burma-Tibet Frontier) *eucyclia*
 EE. Scape 2-9 flowered, usually much taller than the leaves; corolla-limb about 10 mm. diam. (Sikkim, S. Tibet) *vaginata*
 CC. Petiole without vaginate base; lamina hairy on the veins below:
 D. Leaves lobed at least to the middle:
 E. Leaves lobed to the middle, ultimate segments $\pm$ obtuse; corolla-limb 2-2.5 cm. diam. (S.E. Tibet) *latisecta*
 EE. Leaves lobed to $\frac{2}{3}$ or $\frac{3}{4}$ or more; ultimate segments $\pm$ acute; corolla-limb 1.5-2 cm. diam. (Szechwan) *palmata*
 DD. Leaves never lobed as far as the middle:

- E. Corolla hairy:
 F. Inflorescence 1-flowered; lobes of leaf entire or trilobulate and then the lobules entire; calyx about 7 mm. long; corolla-limb about 1.5 cm. diam. (Turkestan) *Minkwitziae*
 FF. Inflorescence more than 1-flowered; leaves shallowly or obscurely lobulate with the lobules broadly and indistinctly crenate, or margin merely wavy; calyx 8-12 mm. long; corolla-limb 3 cm. diam. (Japan) *kisoana*
 EE. Corolla glabrous:
 F. Flowers heteromorphic:
 G. Leaf-lobules and teeth more or less acute:
 H. Leaf 7-9-lobulate; scape with 1-4 umbels each of 2-12 flowers:
 I. Scape with as many as 4 superposed umbels each with 2-8 flowers; only occasionally with one umbel:
 J. Corolla-tube 1-2 times the calyx; leaves orbicular, deeply cordate (Japan) *jesoana*
 JJ. Corolla-tube 2-3 times the calyx; leaves reniform, shallowly cordate (Korea and Manchuria) *Loeseneri*
 II. Scape usually with one umbel of 2-12 flowers, only occasionally with two umbels (Himalaya and Yunnan) *geraniifolia*
 HH. Leaf 5-7-lobulate; scape always with a solitary umbel of 2-3 flowers (Tibet, Szechwan, Kansu) *alsophila*
 GG. Leaf-lobules and teeth rounded or obtuse (Szechwan) : *heucherifolia*
 FF. Flowers monomorphic (Szechwan and Yunnan) *septemloba*
 BB. Flowers yellow; inflorescence racemose *Pauliana*

SUBSECTION EU-CORTUSOIDES.

- P. cinerascens** Franch. in Journ. de Bot., ix, 448 (1895); Diels in Engl. Bot. Jahrb., xxix, 520 (1900); Pax in Engl. Pflanzenr. Primulaceae, 24 (1905); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 132, 145 (1913); Forrest, *ibid.*, xli, 201 (1915); W. W. Sm. and Forrest, *ibid.*, liv, 16 (1929), and in Notes Roy. Bot. Gard. Edin., xvi, 19 (1928). *P. violodora* Dunn in Gard. Chron., xxxii, 129 (1902); Pax in Engl. Pflanzenr. Primulaceae, 27 (1905); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 138, 145 (1913). *P. cinerascens* subsp. *violodora* (Dunn) W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 19 (1928), and in Journ. Roy. Hort. Soc., liv, 16 (1929). *P. riparia* Balf. f. et Farrer in Notes Roy. Bot. Gard. Edin., ix, 40 (1915). *P. neurocalyx* subsp. *riparia* (Balf. f. et Farrer) W. W. Sm. and Forrest, *ibid.*, xvi, 27 (1928), and in Journ. Roy. Hort. Soc., liv, 20 (1929).

Franchet based his description of this species on material collected by Farges about 1893 in woods near Tchen-kéou-tin. The type,

Farges 551, is in the Paris Herbarium and there are co-types at Kew and Edinburgh. Tchen-kéou-tin, otherwise Chengkow, is in the extreme north-east corner of Szechwan and thus very near the borders of Shensi. Franchet associated his species, but only in very general terms, with *P. Listeri* and *P. Gambeliana*. The pertinent points in his diagnosis are "limbus pube brevi cinerascens, . . . suborbiculatus vel ovatus, obscure vel conspicue sinuato-crenatus, crenis minute denticulatis; inflorescentia 3-8-flora . . . calyx 7-8 mm. longus, fere glaber, . . . e basi acuta campanulatus."

For a long time the *Farges* specimens, the results of one collecting, represented all that was available, nor have we met with any further record of the species from the province of Szechwan. Plants secured in Hupeh and in Yunnan, obviously akin, have been described under other names—*P. violodora*, *P. sinomollis*, and *P. sylvicola*. Their status in relation to *P. cinerascens* entails discussion at some length. The literature cited under *P. cinerascens* is confined in its comments to the *Farges* originals and can be briefly dealt with. Pax (*l.c.*) contrasts the species with *P. Rosthornii* and *P. pycnoloba*, but apparently did not see any specimen of it. He follows in the main Franchet's description but makes the calyx "late campanulatus" in opposition to Franchet who is correct. Balfour (*l.c.*) with greater precision classes the species with *P. mollis* and in close proximity to *P. sinomollis* and *P. violodora*. The two latter are assessed by Smith and Forrest (*l.c.*) as subspecies of *P. cinerascens*, and how far this is warranted must be considered after their history is given.

P. violodora is a native of Hupeh and was collected by Wilson in 1900 on mountain cliffs at 1300-2000 m. The type in Kew Herbarium is *Wilson* 923, and what is known of this plant is practically restricted to Dunn's diagnosis and to one sheet. The material under *Wilson* 923 was presented by Messrs. Veitch to Kew, and of the four sheets only one is marked *P. violodora* in Dunn's handwriting—the type. Dunn placed his species near *P. mollis* and made the apposite remark that it is probably rare as it was not met with by Dr. Henry in his extensive exploration of the flora of Hupeh. The type sheet bears two of Wilson's tickets—one gives pink and the other mauve for the corolla. Another sheet, but not in Wilson's handwriting, gives purple—and the locality Chienchi. This suggests that the four sheets were not collected exactly at the same time and place but were given the same number. All may not have been seen by Dunn—as one is written up by Wilson as *P. violodora* and the other two are simply annotated "near *P. violodora*".

dora." Thus is implied a certain doubt as to the homogeneity of the material. Dunn's description is entirely in accord with the type but not with the other three sheets under the same number. When *P. violodora* was described, there was no *P. cinerascens* at Kew for comparison and there does not appear to be any valid distinction between them. Wilson subsequently (in July 1907) collected at Hsing-shan Hsien in Western Hupeh material under No. 103 (at Kew and at Edinburgh) referable equally to *P. cinerascens* and *P. violodora*. The latter is a synonym. But these other sheets under 923 represent something else which is not *P. cinerascens*. They are matched by specimens collected by Chow in Hupeh in 1934 and have a very distinct facies. They deviate too much from *P. cinerascens* to be included within that aggregate and are referred to later under *P. violaris* (*q.v.*).

What then of *P. sinomollis* and *P. sylvicola*? *P. sinomollis* was discovered by Forrest in 1910 growing at 2300 m. on the western flank of the Salween Valley in Lat. 25° 5' N. At the Primula Conference of 1913 Balfour (*l.c.*, 145) gave it the above name and associated it with *P. cinerascens* and *P. violodora*. No description was then published, but a figure shows a young plant of it in culture just coming into flower. It is stated that "all these plants (*i.e.* the three) have petiolate rounded leaves, gray through covering of hairs, and long scapes with tiers of red flowers, each flower with a cup-shaped to campanulate ribbed calyx forming straight erect lobes hardly accrescent." The diagnosis appeared in 1915, and the habitats cited include dry shady situations in mixed and pine forests and pastureland in side valleys. *Forrest* 5523 is the type number. The plant was placed by Balfour in his small section *Mollis*, to be distinguished from its nearest ally, *P. cinerascens*, by the larger rugose leaves and by the elongate many-whorled scapes. But of this ally, all that was then available for comparison was the meagre co-type of the Farges originals. In this same year appears a note by Forrest (*l.c.*, 201) in which he speaks of *P. sinomollis* as one of the finest new species of the region (N.W. Yunnan) and adds that *P. cinerascens*, a shade-loving woodland species with rose-coloured flowers, is also found on the surrounding hills. (What he had in mind was either the plant later described as *P. seclusa* or more probably a dwarf state of *P. sinomollis*.) The ample material of *P. sinomollis*, collected almost entirely by Forrest and wholly from Yunnan is consistent, varying only in size—nor is there anything else near akin in the province except the very distinct *P. mollis*. The larger specimens run to ten whorls of flowers, the

smaller may have but a single umbel and cannot be entirely dissociated from *P. cinerascens* as exemplified by the Farges material. These considerations induced Smith and Forrest (*l.c.*) in 1928 to place *P. sinomollis* within the aggregate of *P. cinerascens*. There remains *P. sylvicola*. In 1915, in Journ. Roy. Hort. Soc., xli, Proc., p. xl, it is reported that Messrs. Wallace showed a new *Primula* raised from seed collected by Forrest in Western China and named *P. sylvicola* by Professor Balfour. It is given a short English description and allocated a place near *P. mollis*. The tale is continued by Forrest in 1916 (Gard. Chron., lix, 318) who mentions it in the same sentence as *P. sinomollis*, records that in the wild it may have ten whorls of flowers and in culture up to seventeen. His photograph of the plant in nature is also reproduced. The next mention was in 1918 when it appeared in Bot. Mag., 8762, as *P. sylvicola* Hort. ex Hutchinson with a complete diagnosis which was based on a robust plant given to Kew by Messrs. Wallace. It is contrasted with *P. sinomollis*. Now Forrest never sent home seeds of a fine *Primula* without securing at the same time adequate dried specimens. Later in 1928 (Smith and Forrest, *l.c.*) he was unable to indicate any of his numbers which represented to him *P. sylvicola* as distinct from *P. sinomollis*, and provisionally both were put together within *P. cinerascens*. It is clear from the above references that Forrest himself favoured at first the view that two distinct plants were concerned and he alone presumably had seen both in the field, but his final opinion as stated to one of the present authors was that only one unit is in question and with that opinion we agree. The relationship between *P. cinerascens* and *P. sinomollis* is so close that it seems better to regard the latter as a subspecies. In general it deviates in the larger size, in the numerous verticels, in the more hairy calyx with membranous interstices between the ridges, and also in its geographical separation. There is no evidence of its occurrence in the broad zone of country between N.W. Yunnan and distant Hupeh and N.E. Szechwan. It grew well in cultivation during 1913-18, but was lost not long after.

There remains to be considered *P. riparia* which is almost certainly synonymous. This plant was collected by Farrer in Kansu in 1914 and was taken by him to be a close associate of *P. obconica*. It was described by Balfour (*l.c.*, 40) and in his view to be regarded as possibly a microspecies of *P. neurocalyx*. His opinion was based on material, in the herbaria of Kew and of Edinburgh, then believed to represent *P. neurocalyx* and no doubt collected at Tchen-kéou-tin

(Chengkow). But Farges found *P. cinerascens* at the same station, and some of the duplicates of that species must have been issued as *P. neurocalyx*. Consequently the comparison advocated by Balfour must be read as a comparison with *P. cinerascens*. The type material of *P. riparia* is quite in accord with the Farges material of *P. cinerascens* and both represent slender states of the species. On the type sheet is written a subsequent comment by Balfour—"note how like to *P. cinerascens*." Farrer records the rarity of the species in Kansu (Balfour, *l.c.*, 40), and reference has been made above to its sparse occurrence in Szechwan and Hupeh.

P. cinerascens is a hairy perennial with a short and usually thin or sometimes rather stout rhizome. Leaves including the petiole 5-16 cm. long; lamina 1.5-9 cm. long and broad, suborbicular to broadly ovate-rotundate, cordate at the base, obscurely or distinctly sinuate-crenate with the crenations minutely denticulate, dark green and pubescent above, paler and conspicuously cinerascens-pilose below; midrib and 4-5 pairs of pinnate lateral nerves slightly impressed above, prominent below; reticulation more or less obscure; petiole 2-9 cm. long, thickly covered with long articulated hairs. Scape 10-25 cm. long, erect, lanate at base, puberulous at apex, thickening and lengthening at fruiting time, carrying an umbel of 3-10 flowers or occasionally two superposed umbels; bracts 4-8 mm. long, linear to lanceolate, puberulous; pedicels 1-3 cm. long, hairy or merely puberulous, thickening and lengthening at fruiting time. Calyx 5-10 mm. long, campanulate to tubular-campanulate, almost glabrous or quite distinctly pubescent, prominently nerved, cut to the middle or a little below into lanceolate often spreading teeth, each with one main and 1-2 pairs of lateral veins. Corolla rose-purple to pink, annulate, heteromorphic; tube only a little longer than the calyx or nearly twice as long, cylindrical, amplate above insertion of stamens; limb 1-2 cm. in diameter with obovate emarginate lobes. Stamens, with anthers 1.5 mm. long, inserted at apex of corolla-tube in thrum-eyed flowers, towards middle of tube in pin-eyed. Long style almost reaching the annulus; short style half the length of corolla-tube. Capsule ovate, shorter than calyx or (ex Franchet) a little longer, dehiscing by longitudinal valves. Seeds not seen mature.

Represented in the Edinburgh Herbarium by the following:—

SZECHWAN: Tchen-kéou-tin (*Farges*, 551—*co-type*).

W. HUPEH: Hsing-shan Hsien (*Wilson*, 103); sine loc. (*Wilson*, 923—*pro parte*—*co-type* of *P. violodora*).

KANSU: Above and below Chago (*Farrer and Purdom*, 33—type of *P. riparia*).

- P. cinerascens** Franch. subsp. **sinomollis** (Balf. f. et Forrest) W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 19 (1928), and in Journ. Roy. Hort. Soc., liv, 16 (1929). *P. sinomollis* Balf. f. et Forrest in Notes Roy. Bot. Gard. Edin., ix, 44 (1915); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 137, 145, fig. 48 (1913)—nomen: Forrest, *ibid.*, xli, 201 (1915). *P. sinomollis* var. *alba* Balf. f. et Forrest in Notes Roy. Bot. Gard. Edin., ix, 45 (1915). *P. sylvicola* Hutchinson in Bot. Mag., t. 8762 (1918). *P. cinerascens* subsp. *sylvicola* (Hutchinson) W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 19 (1928), and in Journ. Roy. Hort. Soc., liv, 16 (1929). *P. sylvicola* Balf. f. ex Journ. Roy. Hort. Soc., lxi, Proc., p. xl (1915)—nomen; Forrest in Gard. Chron., lix, 318, fig. 139 (1916)—nomen.

Leaves including the petiole 5–20 cm. long; lamina 3–14 cm. long, 3–8 cm. broad, very broadly elliptic to suborbicular, cordate at the base, sinuate-crenate or crenate-lobulate, sometimes obscurely so and hydathode-denticulate at the margin, dark green and thinly covered above with articulated hairs, pale green below and densely covered, especially along the veins, with long septate outward-spreading hairs; nerves slightly impressed above; midrib and 6–8 pairs of lateral nerves prominent below; reticulation usually rather open and poorly developed; petiole 1–15 cm. long, thick, very densely pinkish-hirsute and slightly sheathing at the base. Scape 10–60 cm. tall, 1–6 or even more to each plant, villous, carrying from 2–10 superposed whorls of flowers, or in culture up to 17 whorls, with 3–9 flowers in each; bracts 6–8 mm. long, linear to linear-lanceolate, pilose; pedicels 7–15 mm. long, occasionally up to 30 mm., pilose, horizontal or half-erect. Calyx 5–6 mm. long, turbinate-campanulate, pilose without, markedly 5-nerved, cut to the middle into narrowly lanceolate acute and often recurved lobes. Corolla bright rose to magenta-rose or deep purplish-rose with a greenish-white or yellow eye, annulate, heteromorphic; tube usually twice the length of calyx, occasionally about as long as calyx, cylindrical, faintly ampliate above insertion of stamens; limb 1–1.5 cm. in diameter with obovate to orbicular-obovate emarginate lobes. Stamens, with anthers 1.5 mm. long, inserted in middle of corolla-tube in pin-eyed flowers, near apex in thrum-eyed. Long style as long as corolla-tube or slightly exserted; short style barely

as long as calyx. Capsule oblong, not quite as long as calyx, dehiscent by longitudinal valves. Seeds. . . .

The subspecies is represented in the Edinburgh Herbarium by the following collections:—

YUNNAN: Western flank, Salwin valley above Ho-moo-chu (*Forrest*, 5523—*type*); Salwin valley (*F.* 19346, 29523); Shweli-Salwin divide (*F.* 9855, 21103, 24385); hills to east of Tengyueh (*F.* 7569, 7619, 12296); hills three days south of Tengyueh (*Harding*, 26312); sine loc. (*Forrest*, 9807); Lung-ling Hsien (*Tsai*, 56466).

P. cortusoides Linn. Spec. Pl., Ed. 1, i, 144 (1753); Gmelin, Fl. Sibir., iv, 85, t. 45 (1769); Bot. Mag., t. 399 (1797); Andrews, Bot. Rep., i, t. 7 (1797); Jacq. Hort. Schoenbrunn., iii, 5, t. 259 (1798); Lehmann, Monogr. Primul., 23 (1817)—*pro parte*; Maund, Bot. Gard., ii, t. 39 (1827–28); Ledebour, Fl. Alt., i, 208 (1829); Duby in DC. Prodr., viii, 36 (1844)—*pro parte*; Ledebour, Fl. Ross., iii, 8 (1847)—*pro parte*; Turcz. Fl. Baical-dahur. in Bull. Soc. Nat. Mosc., xxii, 291 (1849); Rev. Hort., Sér. iv, viii, 319 (1859); Herder in Acta Hort. Petrop., i, 384 (1872)—*pro parte*; Regel, *ibid.*, iii, 129 (1874)—*pro parte*; The Garden, ix, 107, with fig. (1876); Scheutz, Plantae Vasculares Jenisseenses, 138 (1888); Pax in Engl. Bot. Jahrb., x, 168 (1889)—*pro parte*; Korshinsky in Mém. Acad. Sc. St. Pétersb., vii, 283 (1896); The Garden, lxii, 217, with fig. (1902)—*pro parte*; Pax in Engl. Pflanzenr. Primulaceae, 27 (1905); Takeda in Notes Roy. Bot. Gard. Edin., viii, 84–85 (1913), sub *P. Sieboldii*; Balf. f. in Journ. Roy. Hort. Soc., xxxix, 128, 140, 168–70, 175–77 (1913); W. W. Sm. and Forrest, *ibid.*, liv, 16 (1929); Gould, *ibid.*, liv, 71 (1929); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 19 (1928); Turkevich, Fl. Ross. Asiat., 8 (1923); Busch in Fl. Sib. et Orient. Extra., iv, Cem. 65: 12, fig. p. 16 (1926); Cox and Taylor, Primulas, 61, 96 (1928); Bruun, Cytological Studies in Primula, 21, 28, 125 (1932). For further citations of Russian works to which we have not access, see Busch (*l.c.*, 13). *P. cortusoides* var. *genuina* Turcz. Fl. Baical-dahur., ii, 224 (1847); Busch in Fl. Sib. et Orient. Extra., iv, Cem. 65: 13 (1926). *P. cortusoides* var. *a typica* Regel in Acta Hort. Petrop., iii, 129 (1874)—*pro parte*; Pax in Engl. Pflanzenr. Primulaceae, 27 (1905). *P. cortusoides* var. *a typica* Pax, *ibid.*, 27 (1905). *P. cortusoides* var. β *dentiflora* (Andr.) Pax, *ibid.*, 27 (1905). *P.entiflora* Andrews in Bot. Rep., vi, t. 405

(1804). *P. dentata* Donn ex Roem. et Schult. Syst. Veg., iv, 133 (1819). *Androsace primuloides* Mönch, Meth. Suppl., 152 (1802). *Aleuritia cortusoides* Spach, Hist. Veg. Phanér., ix, 361 (1840).

This species was described by Linnaeus himself from material obtained from Siberia by Gmelin. Its resemblance to *Cortusa* suggested the specific name and it was even suspected (Gmelin, *l.c.*) that it was a hybrid between *Cortusa Matthioli* and a *Primula* of the *Auricula* section! The history of the species is somewhat involved, chiefly because for many years there were included within it plants which later were known as *P. Sieboldii*, *P. saxatilis*, and *P. patens*. It may therefore tend to clearness if a chronological sequence is followed in the comments. The true species came into cultivation in this country in 1794 when seeds were sent by Professor Pallas from Siberia to Lee & Kennedy, a Hammersmith firm, and in 1797 it was twice figured. In the following year in the illustration by Jacquin (*l.c.*) three tiers of flowers are represented—"per culturam scapo bis proliferò luxuriantem." There is also in the figure a hint of the longer pedicels which serve somewhat doubtfully to distinguish *P. saxatilis*. Duby (*l.c.*) quotes its occurrence in Japan, but Thunberg's record of 1784 (Fl. Jap., 82) is now known to concern *P. Sieboldii*. The reference to Turczaninow (*l.c.*, 291) is of moment for that author divides the species into two varieties; one *genuina* is the Siberian plant, the other *patens*—minus villosa, involucris calycibusque glabriusculis, lobis calycinis patentibus—is found in the moist meadows of Dahuria by the river Argun where the former was not seen. Thus Turczaninow described as a variety a plant to which previously in a catalogue (Bull. Soc. Imp. Nat. Mosc., 99 (1838)) he was inclined to accord specific rank. Whether it is so entitled or whether it falls to be included within *P. Sieboldii* is discussed later. The publication by E. Morren in 1873 of a complete description of *P. Sieboldii* (*q.v.*) served in great measure to simplify the problem. In his admirable statement he showed conclusively that the Japanese plant could not be ascribed to *P. cortusoides* even as a variety. Still in 1889 in his first treatment of the genus Pax (*l.c.*, 168) gives *P. cortusoides* as native to Japan, but in his Monograph in 1905 (*l.c.*, 27) the distribution is very correctly stated as extending from the Urals to the Altai and excluding Transbaicalia, Amurland, and Japan. Certain points of importance concerning *P. cortusoides* emerge from Takeda's paper (*l.c.*) on the Japanese Primulas. He shows that *P. Sieboldii* can readily be distinguished from the older species by the almost

glabrous and markedly accrescent calyx with patent lobes; that *P. Sieboldii*, described from cultivated material, has a wild form for which he suggests the name *forma spontanea*; that this form is identical with what Turczaninow called *P. cortusoides* var. *patens* and thus is found in N.E. Asia as well as in Japan. The rest of the story of Turczaninow's plant should come properly under *P. Sieboldii* but it is expedient to complete it here. Pax (*l.c.*, 27) thought it might come under *P. saratilis*, in which view he was followed by Smith and Forrest (*l.c.*), but it is a wrong interpretation. The name *P. patens* Turcz. has been revived comparatively recently by two Russian botanists. Turkevich (*l.c.*, 9) gives it status as a species and contrasts it with *P. cortusoides*. Busch (*l.c.*, 17) supplies a complete diagnosis, a figure and a map showing distribution. But neither author deals adequately with the previous literature on the wild and cultivated forms of *P. Sieboldii* nor is there any reference to Takeda's competent analysis of the record. It does not seem possible to challenge the priority of the name *P. Sieboldii* nor to show that the wild form in Japan is essentially different from the plant of Transbaicalia and the Amur. The latest variation in nomenclature concerning the wild plant is by Kitagawa (*Lineamenta Fl. Mansh.*, 353 (1939)) who makes it *P. Sieboldii* f. *patens* (Turcz.) Kitagawa.

The nearest ally of *P. cortusoides* is without doubt *P. saratilis*, and the narrow distinction between them is discussed under that species which is more frequently seen in culture than *P. cortusoides*.

A more or less hairy perennial with a short comparatively stout rhizome. Leaves including the petiole 6-26 cm. long; lamina 2-9 cm. long, 1.5-6 cm. broad, ovate to oblong in outline, deeply cordate at the base or subcordate, rounded or obtuse at the apex, incised-crenate-lobate at the margin, the lobes irregularly denticulate, thickly or thinly pubescent above, sparsely or densely villous below; midrib and 4-6 pairs of pinnate lateral nerves slightly impressed above, prominent below, reticulation open and poorly developed; petiole 3-19 cm. long, usually coated with numerous long articulated hairs. Scape 10-50 cm. tall, almost glabrous or markedly villous especially in the lower half, carrying an umbel of 2-15 flowers; bracts 4-7 mm. long, lanceolate to almost subulate, softly villous and with one main nerve; pedicels 5-10 mm. long, pilose or almost glabrous, at fruiting time thickening and lengthening to 2.5 cm. Calyx 5-7 mm. long, tubular to tubular-campanulate, glabrous or puberulous to softly pilose, cut to the middle into erect

lanceolate acute lobes each with one prominent main nerve and occasionally with a pair of faint lateral nerves. Corolla rose or red to rose-violet, annulate, heteromorphic; tube slightly longer than the calyx up to nearly twice as long, cylindrical, ampliate above insertion of stamens; limb 1.5-2 cm. in diameter with obcordate emarginate lobes. Stamens, with anthers 1.5 mm. long, inserted at apex of corolla-tube, almost touching the annulus, in thrum-eyed flowers, near middle of tube in pin-eyed. Long style almost the length of corolla-tube; short style half as long. Capsule oblong, almost half as long again as calyx, dehiscing by longitudinal valves. Seeds about 1 mm. in diameter, somewhat flattened and discoid, quadrate-angled to ovoid, reticulate-surfaced.

This species is represented in the Edinburgh Herbarium by the following collections:—

SIBERIA: Altai (*Prescott* in 1830): Tomsk (*Kuznezow*, 18); Mariinsk and Atschinsk (*Arnell* in 1876): sine loc. ex Herb. Fischer.

MONGOLIA: Alashan (*Przewalski* in 1873).

EUROPEAN RUSSIA: Ufa (*A. A. Bulavkina* in 1912).

var. **tomentella** Regel in Acta Hort. Petrop., iii, 130 (1874); Pax in Engl. Pflanzenr. Primulaceae, 27 (1905); Busch in Fl. Sib. et Orient. Extra., iv, Cem. 65: 14 (1926). *P. cortusoides* f. *tomentella* Regel: Turkevicz in Fl. Ross. Asiat., 9 (1923).

Differing from the type in the leaves being completely silvery-pilose and the calyx at flowering time white-pilose.

The variety is not represented in the Edinburgh Herbarium.

P. Kaufmanniana Regel in Acta Hort. Petrop., iii, 131 (1874), and in Fl. Turkest. (Bull. Soc. Friends Nat. Hist. Anthropol. and Ethnogr., xxi, 11), i, t. 4 (1876); Trautvetter in Acta Hort. Petrop., ix, 6 (1884); Pax in Engl. Bot. Jahrb., x, 169 (1889), and in Engl. Pflanzenr. Primulaceae, 28 (1905); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 140, 168-70 (1913); Fedtsh. in Conspectus Fl. Turkest., pt. v, 2 (1913); Farrer, Engl. Rock Garden, ii, 147 (1919); Turkevicz, Fl. Ross. Asiat., 11 (1923); The Garden, lxxxvii, 209 (1923); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 19 (1928), and in Journ. Roy. Hort. Soc., liv, 16 (1929); Kesselring in Gartenflora, lxxvi, 270, with fig. (1927); Cox and Taylor, Primulas, 96 (1928). *P. cortusoides* Herd. in Regel et Herd. Enum. Pl. Semen. in Bull. de la Soc. d. Nat. de Mosc., i, 60 (1869). *P. Kaufmanni* Regel Reisebriefe in Bull. Soc. Nat. Mosc., 185, 186, 189 (1878).

P. Kaufmanniana f. *albiflora* B. Fedtsch. in *Conspectus Fl. Turkest.*, pt. v, 2 (1913); Turkevicz, *Fl. Ross. Asiat.*, 12 (1923).

The material in the Leningrad Herbarium on which this species is based was collected by Semenow near Kopal to the west of the river Ili, at the Zauku Pass in the Thian Shan and in Turkestan. It is known from the Alexander Mountains, from Samarkand, Bukhara, and Ferghana. It is recorded from elevations of 1000–3700 m. In 1876 Regel (*l.c.*) gave a second description along with an excellent figure and took the opportunity of correcting his previous statement as to the ultimate length of the bracts—demum iis (pedicellis) duplo breviora. Pax (*l.c.*, 28) placed the species aptly enough between *P. mollis* and *P. polyneura*. The nearest of kin is undoubtedly *P. lactiflora*, also from Turkestan, and the distinctions between them will be found under that species. A white form of *P. Kaufmanniana* is described by Fedtschenko (*l.c.*). The species itself is stated to have come into cultivation in this country in 1883 (The Garden, *l.c.*), but no details are given. It was introduced to Edinburgh Botanic Garden in 1905 (Balfour, *l.c.*, 169) from seed obtained by Socalski and persisted until about 1927, at which date it was still in culture on the Continent (Kesselring, *l.c.*).

A more or less hairy perennial with a short stout rhizome. Leaves including the petiole 4–20 cm. long; lamina 2–8 cm. long and broad, in outline orbicular, deeply cordate or subcordate-truncate at the base, divided to one-third into 9–11 or even more ovate or broadly oblong lobes, each deeply dentate or sometimes almost lobulate, dark green and glabrous or sparsely pilose above, paler and more or less villous below especially along the nerves; midrib and 4–6 pairs of pinnate lateral nerves impressed above, prominent below; reticulation open and poorly developed; petiole 1.5–12 cm. long, stout, narrowly winged, thickly covered with long pale tawny septate hairs. Scape 8–22 cm. tall, stout, erect, densely or sparsely pilose, carrying one single or two closely superposed umbels with 3–6 flowers in each; bracts 5–10 mm. long, linear-lanceolate or lanceolate to elliptical or obovate, sometimes foliaceous and markedly toothed at the apex, puberulous and minutely glandular-punctulate; pedicels shorter or longer than the bracts, 5–15 mm. long, erect or suberect, glabrous or puberulous. Calyx 4–8 mm. long, tubular or at length subcampanulate, glabrous, covered with minute red striae, cut to the middle into lanceolate acute or subobtusate teeth, each with one prominent main nerve and usually a pair of faint lateral nerves. Corolla violet, rarely white,

faintly annulate, heteromorphic; tube about twice the length of calyx, sometimes a little longer, narrowly cylindrical, ampliate above insertion of stamens: limb 8-18 mm. in diameter with obcordate emarginate lobes. Stamens, with anthers about 1.5 mm. long, inserted at middle of corolla-tube in pin-eyed flowers, at apex in thrum-eyed. Long style as long as or almost as long as corolla-tube; short style half the length of corolla-tube. Capsule. . . . Seeds. . . .

The species is represented in the Edinburgh Herbarium by the following collections:—

TURKESTAN: Semiretchensk Province (*Socalski*, 55); (*Regel* in 1884).

P. lactiflora S. Turk. in Not. Syst. Herb. Petrop., ii, 13 (1921), and in Fl. Ross. Asiat., 12 (1923); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 19 (1928), and in Journ. Roy. Hort. Soc., liv, 16 (1929).

This species appears to have been first collected in Samarkand in several places in the Seravshan Alps (Zarafshan). The type material in Herb. Leningrad (ex Turkevicz) was obtained by Komarov in 1892-93. But both Regel (1882) and Semenoff (1888) are credited with earlier findings. It is known also to occur in Fergana and in Bukhara. Its area of distribution is therefore almost the same as that of its ally *P. Kaufmanniana*, which, however, has a slightly greater extension eastwards. The diagnosis of Turkevicz cites as distinguishing marks the spathulate bracts, the prominent nerves of the calyx and the white corolla-limb with violet tube. These data do not indicate any marked difference between the two species since Fedtschenko has described a white-flowered form of *P. Kaufmanniana* (*q.v.*) with the calyx teeth “eximie nervosae” and subjoined is an account of two varieties of *P. lactiflora* which tend to emphasise the close kinship. The two species, however, have each a definite facies and, apart from the corolla-colour, *P. lactiflora* has thinner more membranous leaves, very slender petioles, scape and pedicels, a narrower corolla-tube and a long exserted style. There is no record that the species has ever been in culture.

A more or less hairy perennial with a comparatively slender or sometimes stout rhizome. Leaves including the petiole 3-16 cm. long; lamina 1-8 cm. long and broad, though usually 4-7 cm., orbicular, markedly cordate at the base, palmately 7-9 lobed to one-third or one-fourth, the lobes lobulate and dentate, dark green and quite glabrous or slightly hairy on the nerves above, paler

green below and markedly hairy, the hairs more numerous along the main veins; midrib and 3-4 pairs of more or less pinnate lateral nerves slightly impressed above, prominent below; reticulation very open and feebly developed; petiole 2-10 cm. long, villous, sheathing at the base. Scape 8-22 cm. tall, very slender, pilose at the base, glabrous or puberulous or pilose at the apex, carrying a single or two superposed umbels with 2-5 flowers in each; bracts 4-9 mm. long, lanceolate to oblong-lanceolate, puberulous and with one main nerve; pedicels 7-22 mm. long, slender, erect or suberect, glabrous or puberulous. Calyx 5-10 mm. long, tubular to sub-campanulate, glabrous or slightly pubescent, conspicuously veined, cut to the middle into lanceolate acute teeth each with 3 main nerves. Corolla with white limb and violet tube, annulate, heteromorphic; tube 2-3 times the calyx, narrowly cylindrical, slightly ampliate above insertion of stamens; limb 1-1.5 cm. in diameter with obcordate deeply emarginate lobes. Stamens, with anthers about 1 mm. long, inserted at middle of corolla-tube in pin-eyed flowers, near apex in thrum-eyed. Long style markedly exserted beyond annulus; short style about half the length of corolla-tube. Capsule (ex Turkevicz) oblong, a little longer than the calyx. Seeds. . . .

The type is in the Leningrad Herbarium and the species is represented in Edinburgh by:—

TURKESTAN: PROV. Fergana; distr. Margelan (*Dessiatoff*, 675).

var. **lactea** Schipezinsky in Not. Syst. ex Herb. Hort. Bot. Petrop., 99 (1921).

The distinguishing features given by the author are simply: "Limb of the corolla white, leaves $\pm$ villous below on the nerves, pedicels glabrous, nerves of the calyx very prominent." The type of the variety was examined by Smith and Forrest in 1928 and their MSS. note states "that the variety differs from typical *P. lactiflora* in the shorter stouter habit, in the shorter heavier and much more flattened petioles, in the lamina thicker in texture and more pilose below, in the stouter scape, in the more prominent bracts, in the denser inflorescence, in the shorter calyx, in the shorter and less deeply coloured corolla-tube, and in the broader and more patent corolla-limb." These features suggest an approach to *P. Kaufmanniana*.

The variety is represented in Edinburgh by:—

BUKHARA: Photographs of type in Herb. Leningrad—*Lipsky* in 1896.

var. **lacticortusoides** Schipeczinsky in Not. Syst. ex. Herb. Hort. Bot. Petrop., 100 (1921).

The distinctions given by the author are: "Limb and tube of corolla violet, leaves below completely villous, pedicels sparsely villous, nerves of the calyx not prominent." Smith and Forrest in a MSS. note state that "the variety is very near the type but is decidedly smaller, the leaves more villous below, the bracts more prominent, the pedicels with a few hairs and short and thus the inflorescence more congested, and the corolla-limb as well as the tube is violet."

The variety is represented in Edinburgh by:—

BUKHARA: Photograph of type in Herb. Leningrad—*Lipsky* in 1897.

P. mollis Nutt. ex Hook. in Bot. Mag., t. 4798 (1854); Morren, Belg. Hort., v, t. 66 opposite p. 65 (1855); Journ. Hort. Prat. Belg., xii, 321 (1855); Fl. des Serres, Sér. II, ii, 97, t. 1230 (1857); Walpers, Annal., v, 465 (1858); Floricult. Cab., 49 (1859); Hook. f. Fl. Brit. Ind., iii, 484 (1882); Garden, xxvii, 597, with fig. (1885); *ibid.*, lxxvi, 425, fig. p. 424 (1912); Pax in Engl. Bot. Jahrb., x, 168 (1889), and in Engl. Pflanzenr. Primulaceae, 28, fig. 16 (1905); Watt in Journ. Roy. Hort. Soc., xxix, 311, 321, fig. 73 E (1904), and *ibid.*, xxxix, 202, 207, 215–216 (1913); Balf. f., *ibid.*, xxxix, 144, 145, fig. 87 (1913); Craib, *ibid.*, xxxix, 186 (1913); W. W. Sm. and Forrest, *ibid.*, liv, 16 (1929), and in Notes Roy. Bot. Gard. Edin., xvi, 19 (1928); Bruun, Cytological Studies in Primula, 23, 125 (1932). *P. mollis* subsp. *seclusa* (Balf. f. et Forrest) W. W. Sm. et Forrest in Notes Roy. Bot. Gard. Edin., xvi, 19 (1928), and in Journ. Roy. Hort. Soc., liv, 16 (1929). *P. seclusa* Balf. f. et Forrest in Notes Roy. Bot. Gard. Edin., ix, 44 (1915); Ward in Journ. Roy. Hort. Soc., xlix, 151, 153 (1924); Gard. Chron., lxxxviii, 8 (1930); Bruun, Cytological Studies in Primula, 23, 125 (1932).

This very distinct species was discovered in the mountains of Bhutan about 1852–3 by Booth who sent ripe seeds of it to his friend Nuttall. Plants raised by the latter flowered in April 1854 and were given the name *P. mollis*. The species attracted immediate attention and was described and figured by Hooker (*l.c.*) in the same year. It was placed "intermediate as it were between *Primula sinensis* and *P. cortusoides* but very different from either in foliage, corolla, and especially calyx." From this introduction

by seed our gardens were peopled and the plant was not seen again in the wild until 1905 (Craib, *l.c.*). It grows in shady situations on the margins of thickets and big streams at elevations of 2300-3300 m. Until 1913 all the plants in culture were descendants of the Booth originals, but in that year it was found in Yunnan by Forrest who took it for *P. cinerascens*. His material was described by Balfour as *P. seclusa* (*l.c.*) and plants were raised from Forrest's seed under that name. They appeared to differ from *P. mollis* in their larger leaves and larger calyx. But comparison of both in culture has failed to disclose any valid distinction.

Thus for some fifty years this species was known only from garden material and most of the references of that period add but little to the first description. Its position in the genus has not been in dispute. Pax (*l.c.*) placed it in his section *Sinenses*; Balfour (*l.c.*) tentatively suggested for it a section *Mollis* and its separation from the larger aggregate; Smith and Forrest (*l.c.*) include it in *Cortusoides*, an intermediate aggregate, in which they are followed by Bruun (*l.c.*) dealing with the cytological evidence. But these apparently different views concern sectional values only and not this individual species. Its nearest ally is *P. cinerascens* from which it is readily distinguished by the large calyx and by the usually monomorphic flowers. It is doubtfully hardy even in the milder parts of this country but grows vigorously indoors and ripens seed freely.

A very hairy perennial with a short and usually stout rhizome. Leaves including the petiole 10-30 cm. long; lamina 4-18 cm. long and broad, subrotundate to reniform, deeply cordate at the base, sinuate-lobate and denticulate-crenulate at the margin, dark green and quite heavily coated above with septate hairs, lighter green below and covered with black or reddish sessile glands and long outward-spreading articulated hairs along all the nerves; midrib and 4-6 pairs of pinnate lateral nerves slightly impressed above, prominent below; reticulation open and rather feebly developed; petiole 5-20 cm. long, stout, very markedly lanate. Scape 10-60 cm. tall, as many as 6 to each plant, villous, carrying 2-10 superposed umbels each with 4-9 flowers; bracts 5-15 mm. long, linear-lanceolate, villous; pedicels 1-3 cm. long, stout, villous, half-erect. Calyx 10-12 mm. long, campanulate, softly villous without, usually deep red, prominently veined, cut to the middle into broadly lanceolate to ovate-lanceolate hydathe-apiculate lobes each with 5 nerves. Corolla dark rose to deep crimson, sometimes shaded to maroon at the base, with a yellow or greyish-

green eye, annulate, monomorphic or occasionally heteromorphic: tube usually about as long as calyx, sometimes nearly twice as long, cylindrical, slightly ampliate above insertion of stamens: limb 1-2 cm. in diameter with obcordate, emarginate lobes. Stamens, with anthers 1.5 mm. long, inserted near middle of corolla-tube or slightly higher in monomorphic flowers, almost at the middle in pin-eyed. Style in pin-eyed flowers reaching the annulus and level with the stamens in monomorphic flowers. Capsule broadly oblong, more or less equalling calyx, dehiscing by longitudinal valves. Seeds about 0.75 mm. in diameter, quadrate-angular to subovoid, finely reticulated, obscurely vesicular-surfaced. The type is at Kew and the species is represented in the Edinburgh Herbarium by:—

BHUTAN: Tsekang (*J. C. White*, 54); Sawang, Kurted (*Cooper*, 4227).

ASSAM HIMALAYA: Phuthang, Balipara Frontier (*Ward*, 11444).

UPPER BURMA: Hpawte (*Farrer*, 950); on Htawgaw Bum, north of Htawgaw (*Forrest*, 24565); hills north-west of Htawgaw (*F.* 27027); western flank of N'Maikha-Salwin divide (*F.* 27094, 27286); near Feng-shui-ling pass, divide between Irawaddy system and headwaters of Shweli (*Ward*, 1632); Mount Victoria (*Cooper*, 5974; *R. U.* 3059); Myitkyina (*Kermode*, 17412).

YUNNAN: N'Maikha-Salwin divide (*Forrest*, 18019); Shweli-Salwin divide (*F.* 12059—*type* of *P. seclusa*, 15723); sine loc. (*F.* 29917).

P. polyneura Franch. in Morot, Journ. de Bot., ix, 448 (1895); Pax in Engl. Pflanzenr. Primulaceae, 28 (1905); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 136, 140, 141 (1913); Farrer, Engl. Rock Gard., ii, 169 (1919); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 19 (1928), and in Journ. Roy. Hort. Soc., 16 (1929); Wehrhahn, Die Gartenstauden, ii, 780, 781 (1930); Bruun, Cytological Studies in Primula, 21, 125 (1932). *P. polyneura* subsp. *hymenophylla* (Balf. f. et Forrest) W. W. Sm. et Forrest and subsp. *lichiangensis* (Forrest) W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 19 (1928), and in Journ. Roy. Hort. Soc., liv, 16, fig. 1 (1929); Chen in Bull. Fan Inst. Biol., Bot. Ser., ix, No. 5, 279 (1939). *P. polyneura* subsp. *sataniensis* and subsp. *sikuensis* (Balf. f. et Farrer) W. W. Sm. and Forrest, and subsp. *Veitchii* (Duthie) W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 19 (1928), and in Journ. Roy. Hort. Soc., liv, 16 (1929).

P. Veitchii Duthie in Gard. Chron., xxxvii, 344, with fig. (1905), and in Bot. Mag., t. 8051 (1905); Pax in Engl. Pflanzenr. Primulaceae, 346 (1905); Jardin, xxii, 184 (1908); Tribune Hort., iii, t. 84 (1908); *ibid.*, ix, 105 (1914); Rev. Hort. Belge, xxxvi, 270 (1910); Silva Tarouca, Freiland-Stauden, 194 (1910); Wilson, Veg. West China [Publ. Arn. Arb., No. 2, t. 408 (1911)]; Journ. Roy. Hort. Soc., xxxi, Proc., p. cxxvii (1906); Balf. f., *ibid.*, xxxix, 138, 140-1, fig. 43 (1913); *ibid.*, xlii, 36 (1916); Farrer, *ibid.*, xlii, 93 (1916); Ward, *ibid.*, xlviii, 207 (1923); McLaren, *ibid.*, liv, 66 (1929); Gould, *ibid.*, liv, 71 (1929); Farrer, Engl. Rock Gard., ii, 192 (1919); The Garden, lxxxvii, 209, with fig. (1923); Hand.-Mzt. in Med. Göt. Bot. Trad., ii, 99, 111 (1926); Bruun, Cytological Studies in Primula, 23, 125 (1932). *P. lichiangensis* Forrest in Gard. Chron., l, 473, with fig. (1911); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 132, 134, 140-1, fig. 42 (1913); Forrest, *ibid.*, xli, 206, fig. 74 (1915); Farrer, *ibid.*, xlii, 93, 95, 101, 103 (1916); Tribune Hort., ix, t. 414 (1914); Farrer, Engl. Rock Gard., ii, 149, pl. 14 (1919); The Garden, lxxxvii, 209, fig. p. 208 (1923); Ward in Journ. Roy. Hort. Soc., xlviii, 206-7 (1923); McLaren, *ibid.*, liv, 66 (1929); *ibid.*, lix, 152, Proc., p. xxvi (1934); Cox and Taylor, Primulas, 61, 95-7 (1928); Ward in Gard. Chron., lxxxviii, 8 (1930); Bruun, Cytological Studies in Primula, 23, 125 (1932); Hand.-Mzt. in Symb. Sin., vii, 734 (1936). *P. hymenophylla* Balf. f. et Forrest in Notes Roy. Bot. Gard. Edin., xiii, 11 (1920); Hand.-Mzt. in Journ. Roy. Hort. Soc., liv, 58 (1929), and in Symb. Sin., vii, 734 (1936); Bruun, Cytological Studies in Primula, 125 (1932). *P. sataniensis* Balf. f. et Farrer in Notes Roy. Bot. Gard. Edin., xiii, 18 (1920); Farrer in Journ. Roy. Hort. Soc., xlii, 93, 101 (1916), and in Eaves of the World, i, 217-8 (1917), and in Engl. Rock Gard., ii, 512-3 (1919). *P. sikuensis* Balf. f. et Farrer in Notes Roy. Bot. Gard. Edin., xiii, 18 (1920); Farrer in Journ. Roy. Hort. Soc., xlii, 95 (1916), and in Engl. Rock Gard., ii, 514 (1919). *P. lichiangensis* var. *hapala* Balf. f. et Forrest in Notes Roy. Bot. Gard. Edin., xiv, 47 (1923). *P. cortusoides* var. *lichiangensis* Forrest in Notes Roy. Bot. Gard. Edin., iv, 217, pl. xxvii (1905). *P. saxatilis* var. *pubescens* Pax et K. Hoffm. in Fedde Rep., xvii, 91 (1921).

The material on which Franchet based this species was collected in part by Soulié near Tatsienlu and partly by Prince Henri d'Orléans

on the road from Batang to Litang. *Soulié* 518 in Herb. Paris may be taken as the type. Franchet associated his species with *P. septemloba*, but distinguished it by the narrow form of its calyx with numerous fine nerves. He quoted *P. Kaufmanniana* as even more akin but possessing a glabrous calyx with blunt lobes. The points in his diagnosis, pertinent for our present purpose, are: Folia . . . subtus (nunc dense) cinerascens vel lanuginosa . . . calyx fere cylindricus . . . plus minus pilosus . . . lobis anguste lanceolatis acutissimis vel acuminatis. We believe that *P. polyneura* shows a high degree of variability in size and vigour and particularly in the amount of pubescence or of woolly coating on the underside of the leaves. These variations occur in each of the three provinces of Western China—Kansu, Szechwan, and Yunnan—where the species appears to be fairly common. The long list of synonyms is also an index of this variability, although the multitude of names is in great part due to the paucity of the original material and its absence from most herbaria except that of Paris. It will be convenient to deal with the names in the above sequence.

The type material of *Soulié* is of average vigour, but includes slender states and shows conspicuous white woolly tomentum on the underside of the leaves. Numerous specimens collected in the Tatsienlu area are generally in accord, but the leaves in many cases are pilose only on the nerves below and are neither cinerascens nor woolly, while the petioles are quite shaggy. Pax in his Monograph (*l.c.*, 28) had no specimens before him and in 1913 Balfour (*l.c.*, 140) suspected that *P. Veitchii* and *P. lichiangensis* were but minor forms of *P. polyneura*. Smith and Forrest in their paper on the sections of the genus (*l.c.*, 19) included within *P. polyneura* all the synonyms quoted above as possibly subspecies. Brunn (*l.c.*) found that plants cultivated under three at least of these names did not differ cytologically from *P. polyneura*.

P. Veitchii is the name under which *P. polyneura* has usually been cultivated in this country since its introduction in 1905. Specimens and seeds were secured by E. H. Wilson in 1904 in the mountains of W. Szechwan. The description by Duthie was based on plants flowering in the gardens of Messrs. Veitch and the nearest ally is stated to be *P. cortusoides*. It is safe to say that the description would not have been published had material of *P. polyneura* been available for comparison. The specimen illustrated by Duthie and the collections of Wilson at that period under No. 4051 are of robust plants, but are in agreement in all essentials with the *Soulié* originals. We have not been able to corroborate (even with much

material) the statement of Duthie that the capsule equals twice the calyx, nor is the tube of the latter ovate. These points are mentioned as they apparently led Pax astray (*l.c.*, 346) in his endeavour to place *P. Veitchii* next to *P. sinensis*.

A somewhat similar story attaches to *P. lichiangensis*. This plant was described at first as a variety of *P. cortusoides* by Forrest (*l.c.*), but later given specific rank. The originals from the Lichiang Range (Forrest, 2275) as well as other Yunnan material are as a rule quite robust plants, but such as come from over 4000 m. are similar in vigour to the more northern representatives. What appears at first to be a difference of some moment is the tendency in the majority for the leaves to be pilose only on the nerves beneath. But in due course Forrest found in Yunnan examples of his species with a heavy white tomentum and these were designated var. *hapala* (*q.v.*)—a variety leading back at once to the Tatsienlu plant.

P. hymenophylla is too closely similar to *P. lichiangensis* to permit of any appreciable distinction. In general it is somewhat more glabrescent on the underside of the leaves and the calyx shows the same tendency. But this variation in the degree of tomentum can be seen (in cultivation) in a batch of plants raised from the same capsule of *P. lichiangensis*.

P. sataniensis is a plant from Kansu, and within that northerly province it tends to be of modest dimensions but can be quite robust. The leaves have the sparing pilosity of *P. hymenophylla* and the calyx is in keeping for it is glabrous or almost so. The petioles, scape, and pedicels continue shaggily pilose. The more slender examples are quite the same as the high-level glabrescent forms of *P. polyneura* occurring near Tatsienlu. Farrer's own opinion in the field (*ex scheda*) was that he had secured a variety of *P. polyneura*.

P. sikuensis was collected also in Kansu by Farrer who believed he had *P. lichiangensis* before him. It is less robust as is to be expected, but there is no other distinction. Its leaves are similar to those of *P. sataniensis*, but the calyx is again quite pilose as in the typical *P. polyneura*.

The evidence is therefore on the whole in favour of one large unit. It is true that the extremes present a very different facies to one another, but there is a chain of unmistakable intermediates throughout. As already noted, the three main geographical areas for the species contain the same morphological variations. Cultural experiments do not support the view that the aggregate can be divided into quite distinct entities.

The herbarium specimens cited below give a fairly complete statement of the distribution. The species has an altitudinal range of 2300-4300 m. It is well established in cultivation and is quite hardy.

A densely hairy or almost glabrous perennial with a short thin or stout rootstock. Leaves including the petiole 4-30 cm. long; lamina 2-10 cm. long and broad, occasionally as much as 16 cm., in outline broadly deltoid or ovate to orbicular, deeply cordate to subcordate at the base, 7-11-lobulate, the lobules broadly ovate and subentire to conspicuously dentate or crenate, thinly or sometimes thickly pubescent above, almost glabrous below or with numerous long white septate hairs along the nerves or often thickly plastered with copious white cottony hair, occasionally with reddish hairs; nerves impressed above, midrib and 3-6 pairs of pinnate lateral nerves prominent below or in very hairy forms almost completely hidden behind the dense tomentum; petiole 2-20 cm. long, thinly or thickly pilose. Scape 10-50 cm. tall, slender or stout, sparsely or copiously pilose, carrying usually one, sometimes 2-3 umbels, each with 2-12 flowers; bracts 5-10 mm. long, linear to lanceolate, pubescent or pilose; pedicels 5-25 mm. long, pilose, erect or suberect to nodding. Calyx 5-12 mm. long, tubular and almost cylindric, sometimes slightly inflated at the base, pilose or pubescent, rarely almost glabrous, conspicuously veined, cut to the middle or to slightly below into narrowly lanceolate acute or acuminate ciliate lobes each with 5 usually prominent veins. Corolla pale rose or rich rose-red to crimson, purple or wine-coloured, with a greenish-yellow, yellow or orange eye, annulate, occasionally exannulate, heteromorphic; tube 1-2 times the calyx, usually broadly cylindrical, ampliate above insertion of stamens; limb 1-2.5 cm. in diameter with obcordate, emarginate or sometimes denticulate lobes. Stamens, with anthers 1-1.5 mm. long, inserted near middle of corolla-tube in pin-eyed flowers, at apex, reaching the annulus, in thrum-eyed. Long style as long as corolla-tube or even conspicuously exerted; short style half as long as tube. Capsule usually about as long as calyx, sometimes shorter, sometimes longer, oblong-ovoid, dehiscing at the apex by longitudinal valves. Seeds quadrate-angled to ovoid, 1 mm. in diameter, vesicular-surfaced.

Represented in the Edinburgh Herbarium by the following collections:—

SZECHWAN: Tatsienlu area (*Cunningham*, 555, 556, 557, 558, 562, 564, 606, 612, 648); (*McLaren's Native Collector*, 7); (*Harry Smith*,

1187); Djesi-la and Djesi-Longba, south of Tatsienlu (*Rock*, 17539); mountains around Muli (*Forrest*, 28400); mountains N.E. of Muli (*F.* 21359); Yenching, north of Muli (*F.* 30287); Muti Konka, Muli Territory (*Rock*, 23696, 23729, 24297); Muli district (*Hand.-Mzt.*, 7219); mountains east of Yungning (*Forrest*, 21227); Pa-lang Shan (*Wang*, 21174); west of Wen-Chuan Hsien (*W.* 23113a); Minya Konka Snow Range, east of Yulong Hsi (*Rock*, 17672); Mount Mitzuga, west of Muli Gomba (*R.* 16261, 16506, 23986); mountain between Wa-Erh and Muli Gomba (*R.* 16921); mountain between the Litang and Yalung Rivers (*R.* 16670); mountains north of Baurong and east of the Yalung River (*R.* 17800); Mupin (*Wilson*, 1185—form with reddish tomentum); sine loc. (*W.* 4051); also Tatsienlu (photo. *Soulié*, 518—*type of P. polyneura* in Herb. Paris).

YUNNAN: Eastern flank of the Lichiang Range (*Forrest*, 2275—*type of P. cortusoides* var. *lichiangensis*, 5717, 10036, 30300); Goodo-Shan (*F.* 20535); Labo Shan (*F.* 30311); Haba Shan (*F.* 30209); Bei-ma-Shan (*F.* 13848—*type of P. lichiangensis* var. *hapala*, 13976); (*Rock*, 22837); Moting Shan (*R.* 23341); Yungling (*Forrest*, 30250, 30253, 30254); mountains N.E. of the Yangtze bend (*F.* 10358); Mekong-Yangtze divide (*F.* 19663); Atuntze (*Ward*, 87); Mt. Kaakerpu (*Yü*, 10489); sine loc. (*Forrest*, 18699, 29159, 29241).

S.E. TIBET: Doker La, Mekong-Salwin divide (*Forrest*, 16747—nec 16794 in diagn. orig.—*type of P. hymenophylla*).

KANSU: Satanee and Gahoba Ranges (*Farrer*, 61—*type of P. sataniensis*); Siku Range (*Farrer*, 86—*type of P. sikuensis*); Mir-go Ridge T'ao River (*Purdum*, 178); Ho Lan Shan Mountain (*Ching*, 64); Gargannar, south of old Taochow (*C.* 944); T'ao River basin (*Rock*, 12251, 12316, 12438, 13652).

P. saxatilis Komarov in *Acta Hort. Petrop.*, xviii, 429 (1901); and *ibid.* (Fl. Mansh., iii), xxv, 223 (1907); Pax in *Engl. Pflanzenr. Primulaceae*, 27 (1905)—*pro parte*, excl. syn.; Nakai in *Journ. Coll. Sc. Imp. Univ. Tokyo*, xxxi, 78 (1911); Balf. f. in *Journ. Roy. Hort. Soc.*, xxxix, 136, 140-2, 169, 170, fig. 80 (1913); Takeda in *Notes Roy. Bot. Gard. Edin.*, viii, 84-85 (1913)—*pro parte*, sub *P. Sieboldii*; Bailey, *Stand. Cycl. Hort.*, 2794, fig. 3183 (1916); Farrer, *Engl. Rock Gard.*, ii, 179, plate 23 (1919); The Garden, lxxxiii, fig. p. 556 (1919); *ibid.*, lxxxvii, 208-209 (1923); Turkevicz, *Fl. Ross. Asiat.*, 9, 10 (1923)—in nota sub *P. patens*; Busch in *Fl. Sib. et Orient. Extra.*, iv, Cem. 65: 11 (1926); Cox and Taylor, *Primulas*, 61,

96, with fig. (1928); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 19 (1928); W. W. Sm. and Forrest in Journ. Roy. Hort. Soc., liv, 16 (1929); Hand.-Mzt., *ibid.*, liv, 52 (1929); Bruun, Cytological Studies in Primula, 21, 28, 125 (1932). *P. oreodoxa* Hort. ex Balf. f. (*l.c.*, 170).

P. saxatilis was described from specimens collected in June 1897 by Komarov on cliffs of the elevated basaltic plateau of the Pei-schan (Pai-shan) to the east of Mukden in Manchuria and within the boundaries of Northern Korea. The plants were growing in rock-fissures rich in humus. Komarov states that his species is akin to *P. cortusoides* and to *P. Sieboldii*, but leaves the distinctions to be inferred from his detailed diagnosis, in which one pertinent point appears to be the length of the pedicels, a character used later by Pax (*l.c.*, 21) in his key. The latter in his Monograph (*l.c.*, 27) was unable to avail himself of the Komarov originals, but included within his citations an Amur plant collected by Korshinski and an Alashan plant of Przewalski. The former is regarded by Turkevicz (*l.c.*) and by Busch (*l.c.*) as *P. patens*, while the Alashan specimens at Kew and at Edinburgh are *P. cortusoides*. Yet the history of the plant (but not of the name) goes much further back. There is good evidence that *P. saxatilis* has been in cultivation for well over one hundred years. Pax (*l.c.*, 27) records it as having been in the Berlin Botanic Garden in 1806. It was included within *P. cortusoides* until Komarov named it and is commoner in culture than that species, from which it is discriminated by the very long pedicels and the consequently looser umbel. The narrowness of this distinction led Balfour (*l.c.*, 169) to suggest that possibly *P. saxatilis* is no more than a microspecies. Takeda (*l.c.*, 84) also discusses the intimate relationship. The more recent Russian writers, Turkevicz (*l.c.*) and Busch (*l.c.*) exclude *P. saxatilis* from the Siberian Flora, and Busch states that in Manchuria and Korea it replaces *P. cortusoides*. Smith and Forrest (*l.c.*) take *P. patens* to be a prior name, but this view cannot be upheld and is discussed under *P. cortusoides*. The cytology of the species (Bruun, *l.c.*) confirms the close association with *P. cortusoides* and *P. Sieboldii* and kinship with *P. polyneura*. A variety, *pubescens*, described by Pax and K. Hoffmann (Fedde Repert., xvii, 91 (1921)) is in the opinion of Handel-Mazzetti equivalent to *P. Veitchii* (*q.v.* sub *P. polyneura*) and is so stated in Göt. Bot. Trad., ii, 111 (1926). We have seen some of the material and see no reason to challenge the reduction.

In addition to Manchuria and Korea there is evidence, though

slight, of the occurrence of *P. saxatilis* in some of the northern provinces of China. In Herb. Kew is a specimen (*Licent*, 5469) collected in N. Kansu; cited below in Herb. Edin. is one record from Shansi; in Herb. Kew is a sheet (*Licent*, 8855) from the neighbourhood of Tientsin in Chihli. *P. saxatilis* is well known in gardens, divides readily and ripens seed freely.

A more or less hairy perennial with a short slender rootstock. Leaves including the petiole 6–20 cm. long; lamina 3·5–8 cm. long, 3–6 cm. broad, oblong to ovate-oblong, deeply cordate to subcordate at the base, incised-lobate at the margin, the lobes subentire or conspicuously crenate-dentate, dark green and sparsely pubescent above, lighter green and pilose below, the hairs most numerous along the veins; midrib and 5–7 pairs of pinnate lateral nerves slightly impressed above, prominent below; reticulation more or less open and poorly developed; petiole 5–15 cm. long, markedly pilose. Scape 10–30 cm. long, 1–6 to each plant, sturdy and erect, pilose, sometimes almost glabrous towards the apex, carrying an umbel of 3–15 flowers or occasionally two superposed umbels; bracts 3–8 mm. long, linear or lanceolate to oblong-lanceolate, pubescent, sometimes markedly dentate towards the apex; pedicels 1–4 cm. long, usually 2–4 cm., slender, more or less erect or semi-pendent, pubescent or puberulous. Calyx 5–6 mm. long, tubular to tubular-campanulate, sparsely pubescent or glabrous, prominently veined, cut to the middle into lanceolate to oblong-lanceolate, erect, acute or obtuse lobes each with one conspicuous main nerve and sometimes with an inconspicuous pair of lateral nerves. Corolla rosy-violet or pinkish-mauve, annulate, heteromorphic; tube about twice the length of the calyx, cylindrical, ampliate above insertion of stamens; limb 1·5–2·5 cm. in diameter with obcordate deeply emarginate lobes. Stamens, with anthers 1 mm. long, inserted near middle of corolla-tube in pin-eyed flowers, towards apex of tube but not touching the annulus in thrum-eyed. Long style exerted beyond annulus; short style half length of corolla-tube. Capsule oblong, a little longer than calyx, dehiscing by longitudinal valves. Seeds about 1 mm. in diameter, irregularly quadrate to ovoid, reticulate-surfaced.

The type is at Leningrad and the species is represented at Kew and at Edinburgh chiefly by material taken from cultivated plants. Specimens from Manchuria and Korea are lacking. The Shansi record quoted below is based on a sheet received from Vienna and identified by Handel-Mazzetti as *P. saxatilis*.

N. CHINA: Shansi, Ou-t'ai-chan, Pic nord (*Chancet*, A. 521).

- P. Sieboldii** E. Morren, Belgique Hortie., xxiii, 97, t. 6 (1873); The Garden, xiv, 466, pl. clv (1878); *ibid.*, xv, 407 (1879); *ibid.*, xxxv, 335, with fig. (1889); *ibid.*, xxxvi, 318, pl. 721 (1889); *ibid.*, lxxii, 326, fig. p. 327 (1908); Wien Ill. Gart.-Zeit., vi, 523, fig. 171 (1881); Gartenfl., xxxv, 216, fig. 15 (1886); Pax in Engl. Bot. Jahrb., x, 168 (1889); Nestler Hautreizende Primeln., 40 (1904); Pax in Engl. Pflanzenr. Primulaceae, 22 (1905); Takeda in Notes Roy. Bot. Gard. Edin., viii, 84, pl. xiv (1913); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 140, 141, 169, 170, 175-7, fig. 81 (1913); Bailey, Stand. Cycl. Hort., 2792, t. 3181 (1917); Farrer, Engl. Rock Garden, ii, 182 (1919); The Garden, lxxxvii, 209, fig. p. 208 (1923); Boynton in Addisonia, x, t. 323 (1925); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., 19 (1928), and in Journ. Roy. Hort. Soc., liv, 16 (1929); Gould, *ibid.*, liv, 71 (1929); Cox and Taylor, Primulas, 97 (1928); Bruun, Cytological Studies in Primula, 21, 125 (1932); Cooper, New Fl. and Silva, v, 267 (1933). *P. Sieboldii* forma *hortensis* Takeda in Notes Roy. Bot. Gard. Edin., viii, 84 (1913). *P. Sieboldii* forma *spontanea* Takeda in Notes Roy. Bot. Gard. Edin., viii, 84 (1913); Makino, Ill. Fl. Jap., 258 (1924), and Gensyoku Yagai Shokubutu (Nature Col. Wild Pl.), i, 25 (1932); Journ. Jap. Bot., iv, No. 4, t. 1 (1927); *ibid.*, viii, No. 2, t. 3 (1932); Terasaki, Nippon Shokubutsu Zufu (Jap. Bot. Illust. Album), 236 (1933). *P. Sieboldii* forma *patens* (Turez.) Kitagawa in Lineamenta Fl. Mansh., 353 (1939). *P. Sieboldii* vars. *alba*, *grandiflora*, *lilacina*, *striata* E. Morren, Belgique Hortie., xxiii, 97 (1873). *P. cortusoides* (non Linn.) Thunb. Fl. Jap., 82 (1784); Besser, Ueber die Flora des Baikals in Flora, xvii, i, Beibl. 22 (1834); Ledeb. Fl. Ross., iii, 8 (1847-49)—*pro parte*; Maxim. Primitae Florae Amurensis, 192 (1859); Radde, Berichte über Reisen im Süden von Ost-Siberien, 551, 621, 623, 632 (1861); Miq. Prol. Fl. Jap., 283 (1867); Herder in Acta Hort. Petrop., i, 384 (1872)—*pro parte*; Regel, *ibid.*, iii, 129 (1874)—*pro parte*; Franch. and Savatier, Enum. Pl. Jap., i, 299 (1875); Freyn, Plantae Karoanae Dahuricae in Oester. Bot. Zeitschr., xli, 29 (1896), and Plantae Karoanae Amuricae et Zeaënsae in *ibid.*, lii, 443 (1902); Petitm. in Bull. Herb. Boiss., vii, 532 (1907); Somoku Dzusetsu, Ed. Makino, iii, t. 18 (1907). *P. cortusoides* forma *lactiflora* Nakai in Journ. Coll. Sc. Imp. Univ. Tokyo, xxi, 78 (1911). *P. cortusoides* var. *amoena* Lindl. in Gard. Chron., 1218 (1862); Bot. Mag., t. 5528

(1865); Floral Mag., iv, t. 249 (1865); *ibid.*, v, 276 (1866); Fl. des Serres, xviii, t. 1923 (1869-70); *ibid.*, xix, t. 1952 (1873); Fl. and Pomol., 193, with fig. (1870); Neubert's Deutsch. Gart. Mag., 225 (1871); Wooster, Alp. Pl. Ser., ii, t. 48 (1874); The Garden, viii, 408 (1875); *ibid.*, ix, 107, 440, 487 (1876); Ill. Gartenzeit. Stuttgart, xxiii, t. 34 (1879); Rev. Hort., 300, with fig. (1892); *ibid.*, 145, fig. 51 (1907); Journ. Hort., Ser. III, xlv, 277 (1902). *P. cortusoides* var. *grandiflora* A. Verschaffelt in Lemaire, Illust. Hort., xvi, t. 599 (1869); Fl. and Pomol., 193, with fig. (1870). *P. cortusoides* var. *patens* Turcz. Fl. Baikal-dahur. in Bull. Soc. Nat. Mosc., xxii, 291 (1849); Korshinsky in Acta Hort. Petrop., xii, 367 (1892); Komarov in *ibid.*, xxv, 222 (1907); Nakai in Journ. Coll. Sc. Imp. Univ. Tokyo, xxxi, 78 (1911). *P. cortusoides* var. *striata* Lindley in Gard. Chron., 1218 (1862); Fl. and Pomol., 172 (1867); *ibid.*, 193, with fig. (1870). *P. cortusoides* var. *typica* Regel in Acta Hort. Petrop., iii, 129 (1875). *P. patens* Turcz. in Bull. Soc. Nat. Mosc., i, 99 (1838)—*nom. nud.*; Trautvetter in Acta Hort. Petrop., ix, 7 (1884); Turkevicz, Fl. Ross. Asiat., 9 (1923); Busch in Fl. Sib. et Orient. Extra., iv, Cem. 65: 17, fig. p. 16 (1926). *P. patens* var. *genuina* and var. *manshurica* Skvortzow in Lingnan Sc. Journ., vi, 219 (1928). *P. saxatilis* Pax in Engl. Pflanzenr. Primulaceae, 27 (1905)—*pro parte*, non Komarov. *P. gracilis* Stein in Samenkatal. Bot. Gart. Breslau, 3 (1881).

The early history of this species is closely interwoven with that of *P. cortusoides*. The first mention of it in botanical literature is by Thunberg (*l.c.*) who recorded it from Japan as *P. cortusoides* in 1784. For nearly a century it continued to be included within that species which was then regarded as distributed from the Urals through Northern Asia to Japan. Their respective territories are no longer held to overlap, and *P. Sieboldii* is confined to Japan, Transbaicalia, Amurland, Korea, and Manchuria. The references cited above under *P. cortusoides* concern either wholly or in part what is now known as *P. Sieboldii*. This delay in differentiation was possibly due to lack of sufficient herbarium specimens, but the advent of *P. Sieboldii* into cultivation in Europe did not at once advocate separation. It was introduced in 1862 by the Chevalier Philip Franz Von Siebold to his garden at Leyden, but the material was taken over by the firm of Veitch of London. The first plants to flower were submitted to Lindley (*l.c.*, 1218) who described them as representing two very distinct varieties of

P. cortusoides. The importations gave evidence of long culture in Japan (in comparison with what later was found to be the wild plant), proved to be a great success in European horticulture and within a decade were propagated in millions. Apposite here is a quotation from Bot Mag., 5528, sub *P. cortusoides* var. *amoena*—"One has but to compare our present figure with the figures quoted above, or with native specimens from the Russian dominions in our herbaria, to justify the preference that must be given to this variety, on account of the size of the foliage and umbels and flowers, and the deep, almost purple colour of the latter. Thunberg, indeed, in his *Flora Japonica*, says of the species, 'Crescit hinc inde in insula Nipon'; but he adds, 'saepe in hortis culta.'" In 1873 appeared Morren's illuminative statement (*l.c.*) in which are comprised a diagnosis of *P. Sieboldii*, a list of some six varieties of it, and a very adequate account of the history of the species as far as then known. Articles in 1879 and again in 1889 in *The Garden* (*l.c.*) show how far the cult of horticultural varieties of this species was carried. In the present century, though still cultivated and admired, it has not its former prominence. The species itself was allocated by Pax (*l.c.*) in 1889 to his section *Sinenses* and emphasis laid on the character of the calyx as a distinction between it and *P. cortusoides*. In 1905 in his *Monograph* Pax (*l.c.*, 22) dealt with it more fully and apart from Japan recorded it from Transbaicalia, quoting *Karo* 339 from Nertschinsk in support. This is a number subsequently cited by Turkevicz (*l.c.*) and Busch (*l.c.*) in their resuscitation of Turczaninow's *P. patens*. The problem is discussed under *P. cortusoides* (*q.v.*) and reasons given for support of the views of Takeda (*l.c.*, 84) who takes *P. patens* to be the wild form of *P. Sieboldii* and thus equivalent to forma *spontanea* Takeda. Apparently no type material has been preserved of Morren's *P. Sieboldii*, described from cultivated plants.

A more or less hairy perennial with a comparatively long slender rhizome. Leaves including the petiole 4-20 cm. long; lamina 2-10 cm. long, 2-7 cm. broad, ovate to oblong-ovate, cordate or occasionally subcordate at the base, rounded at the apex, regularly lobulate and sometimes markedly ciliate at the margin with the lobules crenulate-dentate, dark green and glabrous or pubescent above, paler green and almost glabrous below or softly and often densely hairy especially along the veins; midrib and 6-8 pairs of pinnate lateral nerves slightly impressed above, prominent below; reticulation open, poorly developed; petiole 2-12 cm. long, slightly fleshy, usually conspicuously pilose. Scape 6-30 cm. tall, sturdy

and erect, pilose in the lower half, glabrous or puberulous above, carrying an umbel of 2-15 flowers, but usually 6-10, or occasionally two superposed umbels; bracts 4-10 mm. long, lanceolate to linear-lanceolate, glabrous or pubescent, sometimes covered with minute red striae, and each with one prominent main vein; pedicels 5-40 mm. long, more or less erect, glabrous or puberulous. Calyx 5-12 mm. long, enlarging in fruit, widely campanulate to infundibular, glabrous or subglabrous, prominently nerved, often red-striate, cut to the middle or almost to two-thirds into lanceolate to ovate-lanceolate patent lobes, acute or obtuse at the apex, minutely ciliate at the margin, each with one prominent main vein and 1-2 pairs of subprominent lateral veins. Corolla rose-violet to lilac-purple or deep crimson with a white eye, sometimes pure white, annulate, heteromorphic; tube about twice the length of calyx, cylindrical, ampliate above insertion of stamens; limb 1-3.5 cm. in diameter with broadly obcordate bilobulate lobes, the lobules entire or minutely crenulate. Stamens, with anthers 1-1.5 mm. long, inserted in upper half of corolla-tube, not reaching annulus, in thrum-eyed flowers, near middle of tube in pin-eyed. Long style barely as long as corolla-tube; short style about half length of tube. Capsule round, about half length of calyx, or, ex Busch, more or less ovoid and about as long as calyx, dehiscing at apex by longitudinal valves.

The species is represented in the Edinburgh Herbarium by the following:—

JAPAN: Near Tokyo (*Takeda* in 1903); Yezo, Hidaka, Sarubuto (*Tatewaki* in 1924); sine loc. (*I. J. Hiwag* in 1908).

EASTERN SIBERIA: Transbaical, Nertschinsk (*Karo*, 339).

Material cultivated in Hort. Edin.—some grown from seed collected at Pitsaikou, near Antung, at the Yalu River, Southern Manchuria.

In Herb. Kew apart from Japanese specimens may be noted the following from N.E. Asia:—

KOREA: (*Mills*, 208).

TRANSBAICALIA: One sheet (presumably coll. *Turczaninow*) entitled *Primula patens* Turcz. In humidis lapidosis ad fl. Argun 1830—Dahuria, 1833. These specimens no doubt co-types of *P. cortusoides* var. *patens* Turcz. Schilka (*Maximowicz* in 1859); near Nikolsk (*Komarov*, 1233).

MANCHURIA: between Mukden and Tung-che-shien (*James* in 1886); Fung-chung (*Ross*, 146); near Yalu (*Webster*, 72).

P. violaris W. W. Sm. et Fletcher.*

This species has previously been confused with *P. cinerascens* and its synonym *P. violodora*. It differs from that species in the much larger leaves which are not crenate but markedly dentate-lobulate, recalling those of *P. Pauliana*. Its leaves also tend to be subglabrescent on both sides, although the petioles remain shaggily pilose. There are two records of its collection. The first was in 1900 when Wilson found it near Chienshi in Western Hupeh. As explained under *P. cinerascens* (q.v.), the plants given Wilson's number 923 are in part referable to Dunn's *P. violodora* (which equals *P. cinerascens*) and in part to the present species. The second finding was in 1934 by Ho-Ch'ang Chow at Tzu Kwei Hsien in Hupeh. His material in the Edinburgh Herbarium and in that of the National Wu-Han University has been taken to represent the type so as to avoid any ambiguity which might arise from the quotation of the Wilson number. But the choice in the name is intended to retain the link with *P. violodora*. Both *P. cinerascens* and *P. violaris* appear to be rare in Hupeh, and the paucity of the available collections from that province suggests the need of further exploration before the two species can be adequately compared.

A vigorous species with a short rhizome. Leaves including the petiole 10–25 cm. long; lamina 4.5–13 cm. long, 5–15 cm. broad, orbicular to reniform in outline, deeply cordate at the base, dentate-lobulate at the margin, the lobules broadly triangular and hydathode-denticulate, thinly pubescent above with the hairs longer on the veins, sparingly pilose on midrib and nerves below, elsewhere glabrous or glabrescent; veins slightly impressed on the more or

* **Primula violaris** W. W. Sm. et Fletcher. Sp. nov.

Species sectionis Cortusoides affinisque *P. cinerascens* Franch. a qua foliis multo majoribus ad 15 cm. diametro, altius cordatis dentato-lobulatis haud crenatis, lobulis late triangularibus crebre hydathodo-denticulatis, utrinque subglabrescentibus nec cinerascensibus differt.

Folia petiolo incluso 10–25 cm. longa; lamina 4.5–13 cm. longa, 5–15 cm. lata, ambitu orbicularis vel reniformis, alte cordata, dentato-lobulata lobulis late triangularibus denticulatis, supra ad nervos sparsim pubescens, infra ad costam nervosque plus minusve pilosa, ceterum glabra; petiolus 6–18 cm. longus, dense pilosus. Scapus 10–40 cm. altus, pilosus, umbellas 1–3 plerumque 5–8-floras gerens; bracteae 3–10 mm. longae, lineares vel lineari-lanceolae; pedicelli 1–2 cm. longi, in fructu ad 3 cm. aucti. Calyx 7–12 mm. longus, campanulatus vel tubuloso-campanulatus, glaber vel subglaber, prominenter multinervius, ad medium vel paulo ultra in lobos lanceolatos acuminatos patentem divisus. Corolla roseo-lilacina vel purpurea, annulata, heteromorphica; tubus calyce paulo vel nunc duplo longior; limbus 1.5–2 cm. diametro lobis obcordatis alte emarginatis. Stylus longus tubum corollinum aequans vel paulo brevior; stylus brevis tubum medium haud superans. Capsula seminaque desunt.

less bullate upper surface; midrib and 4-6 pairs of pinnate lateral nerves conspicuous below; reticulation open and rather feebly developed; petiole 6-18 cm. long, stout, densely pinkish-pilose. Scape 10-40 cm. tall, slender or sturdy, pinkish-pilose, carrying 3 superposed umbels each with 2-8, usually 5-8, flowers; bracts 3-10 mm. long, linear to linear-lanceolate, puberulous; pedicels 1-2 cm. long, slender, up to 3 cm. long and thickening at fruiting time. Calyx 7-12 mm. long, campanulate to tubular-campanulate, glabrous or slightly puberulent, very prominently multi-veined, cut to the middle or just below into lanceolate acuminate outward spreading lobes, each with 3 or 5 nerves. Corolla rose-lilac to purple, markedly annulate, heteromorphic; tube a little longer than calyx or twice as long, cylindrical, ampliate above insertion of stamens; limb 1.5-2 cm. in diameter with obcordate deeply emarginate lobes. Stamens, with anthers about 1 mm. long, inserted near middle of corolla-tube in pin-eyed flowers, towards apex in thrum-eyed. Long style as long as corolla-tube or a little shorter; short style half the length of tube. Capsule. . . . Seeds. . . .

Represented in the Edinburgh Herbarium by the following:—

HUPEH: Tzu Kwei Hsien (*Ho-Ch'ang Chow*, 369—*type*); (*Wilson*, 923—*pro parte*).

SUBSECTION GERANIOIDES.

P. alsophila Balf. f. et Farrer in Notes Roy. Bot. Gard. Edin., ix, 4 (1915); W. W. Sm. and Forrest, *ibid.*, xvi, 20 (1928); Farrer in Eaves of the World, ii, 135, fig. facing p. 136 (1917), and in English Rock Garden, ii, 517 (1919), and in Journ. Roy. Hort. Soc., xlii, 98, 102-3 (1916); W. W. Sm. and Forrest, *ibid.*, liv, 17 (1929).

The first collections of this species were made in 1914 by Farrer and Purdom at 3300-4000 m. in S.W. Kansu and in the adjoining Tibetan coniferous forests. The habitat is usually in deep moss, traversed by the long frail stolons of the plant. The general aspect is well shown in the figure given by Farrer (*l.c.*, 136) which is the only one available. The nearest allies are also found in the western provinces of China—*P. geraniifolia*, *P. heucherifolia*, and *P. septemloba*. From these *P. alsophila* is distinguished by the more slender habit, by the subglabrous leaves of very thin texture, and by the 2-3-flowered scape. The species was introduced into cultivation from seeds collected by Farrer, but was never firmly established.

It persisted until 1923, but apparently did not attract much notice as there are no references to it in horticultural journals. There is not likely to be anything unusual in its capsule or in its seed, but neither is available for description. The plant flowered and seeded well at Edinburgh in 1919-20, but nothing was recorded in supplement of the original description.

A slender stoloniferous slightly hairy perennial. Leaves usually only 2-3 to each plant, including the petiole 7-12 cm. long; lamina 2-4 cm. long, 2.5-5 cm. broad, orbicular in outline, deeply cordate at the base, palmately divided to a third into 5-7 dentate or trilobulate lobes, dark green and sparsely pilose above, pale green below with a few hairs in the region of the veins, ciliolate at the margin; midrib and 2-3 pairs of basal or subbasal lateral nerves conspicuous; reticulation wide and poorly developed; petiole 5-9 cm. long with a few scattered white hairs. Scape 10-16 cm. long, slender, pubescent, carrying an umbel of 2-3 flowers; bracts 4-6 mm. long, linear-subulate, pubescent; pedicels 1-2.5 cm. long, pubescent, slender, sub-pendent. Calyx 5-7 mm. long, campanulate, glabrous or minutely puberulous, prominently 5-veined, cut to below the middle into lanceolate acuminate lobes, membranous around the sinuses. Corolla lilac or reddish-purple to wine-coloured, annulate, heteromorphic; tube twice the length of calyx, cylindrical, ampliate above insertion of stamens; limb 1-1.5 cm. in diameter with obcordate deeply emarginate lobes. Stamens, with anthers at least 1 mm. long, inserted at apex of corolla-tube and almost touching annulus in thrum-eyed flowers, in lower half of tube in pin-eyed. Long style as long as corolla-tube or slightly exserted; short style about 1.5 mm. long. Capsule. . . .

In the Edinburgh Herbarium are the following specimens:—

S.W. KANSU and adjoining TIBETAN FRONTIER: Forests round the Bei-Ling (*Farrer*, 178—*type*); Ardjeri (*F.* 197); T'ao River basin, forests of Shiaoku, beyond Adjuan, eastern Minshan (*Rock*, 12819).

SZECHEWAN: Dongrergo (*Harry Smith*, 3786).

P. eucyclia W. W. Sm. et Forrest in Notes Roy. Bot. Gard. Edin., xiv, 41 (1923); Forrest in Journ. Roy. Hort. Soc., xlix, 35 (1924); W. W. Sm. and Forrest, *ibid.*, liv, 17 (1929); Hand.-Mzt., *ibid.*, liv, 61 (1929); Gould, *ibid.*, liv, 71 (1929); *ibid.*, lvi, Proc., p. xvii (1931); *ibid.*, lx, fig. 21 (1935); *ibid.*, lxi, 256 (1936); *ibid.*, lxiii, 312, fig. 74 (1938); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 20 (1928); Wall

in Gard. Chron., lxxxvii, 225, fig. 92 (1930); Ward, *ibid.*, lxxxvii, 287 (1930), and *ibid.*, lxxxviii, 9 (1930); *ibid.*, ci, 22 (1937); Hand.-Mzt., in Symb. Sin., vii, 734 (1936).

The first specimens of this species were collected by Forrest in 1921 in the Tibetan province of Tsarong. According to the finder (*l.c.*, 35) "it grows in crowded colonies, forming mats many yards in extent sheeted with bloom, on stony alpine meadows and is also seen on cliffs." Although Forrest obtained some seed no effective introduction to culture resulted. But in 1926 the species was found again by Ward in that prolongation of N.W. Burma which abuts on the frontiers of Yunnan and S.E. Tibet and from his seed flowering plants were raised, one of which gained an Award of Merit in 1930. It is still scarce in cultivation but has not been entirely lost. From his knowledge of its occurrence in the Seinghku Valley, Ward (*l.c.*, 287), in an informative note on the species, expresses doubt as to the correctness of the altitudinal record given by Forrest—14,000–15,000 feet—and considers the normal to be 10–11,000 feet. But it must be remembered that the altitudinal range of some alpine is very remarkable. Thus in the allied *P. Normaniana* (*q.v.*) the range is between 6700 and 12,000 feet according to Sherriff and Taylor. The only other collector of *P. eucyclia* appears to be Rock who records it in one of his collections as growing on limestone crags at 15,000 feet, and in another on cliffs at 13,500 feet. The species has its nearest ally in *P. vaginata*, but is readily distinguished by the larger flowers which occur almost always in pairs.

A low-growing perennial with a long thin trailing rhizome, often girt at the base with the withered remains of old foliage. Leaves including the petiole 2–8 cm. long; lamina 1–3 cm. long and broad, orbicular, deeply cordate at the base, palmately cut to the middle into 7 lobes, the lobes deeply and acutely dentate, often tridentate, dark green and pubescent above or even scabrid-puberulous, pale green and glabrous or minutely puberulous below, ciliolate at the margin; midrib and 2–3 pairs of basal or subbasal lateral nerves prominent below; reticulation $\pm$ obscure; petiole 1–6.5 cm. long, glabrous, conspicuously vaginate for the basal 5–10 mm. where it is membranous and 3–5 mm. broad. Scape 3–6 cm. tall, slender, minutely puberulous, carrying 1–2, usually 2, flowers; bracts 3–5 mm. long, lanceolate, acute, puberulous; pedicels 5–10 mm. long, slender, puberulous. Calyx 4–5 mm. long, broadly campanulate, glabrous or almost so, cut to the middle into ovate obtuse ciliolate lobes, each with one main nerve. Corolla pale shell-pink

to dark mauve with a yellow or reddish eye, annulate, heteromorphic; tube twice the length of calyx or a little shorter, cylindrical, ampliate above insertion of stamens: limb 10–18 mm. in diameter with obovate bilobulate lobes, the lobules entire or more usually deeply 2–3-dentate. Stamens, with anthers less than 1 mm. long, inserted towards apex of corolla-tube touching or almost touching the annulus in thrum-eyed flowers, near middle of tube in pin-eyed. Long style usually well exerted beyond annulus; short style half the length of corolla-tube. Capsule subglobose, no longer than calyx, dehiscing rather irregularly by longitudinal valves. Seeds about 1 mm. in diameter, often quadrate-angled, somewhat flattened, vesicular-surfaced.

The species is represented in the Edinburgh Herbarium by:—

S.E. TIBET: Tsarong, Salwin-Kiuchiang divide, N.W. of Si-chi-to (Forrest, 21632—*type*, 19868, 20270); Mount Kenichunpo, Salwin and Irrawady divide (Rock, 21956); mountains west of Champutong, Upper Salwin River (R. 22514).

UPPER BURMA: Seinghku Wang (Ward, 6822); valley of the Seinghku (W. 7483).

P. geraniifolia Hook. f. in Fl. Brit. Ind., iii, 484 (1882); Hook. f. in Bot. Mag., t. 6984 (1888); Pax in Engl. Bot. Jahrb., x, 169 (1889), and in Engl. Pflanzenr. Primulaceae, 28 (1905); Watt in Journ. Roy. Hort. Soc., xxix, 301, 307, 321 (1904), and *ibid.*, xxxix, 202, 207, 215–6 (1913); Balf. f., *ibid.*, xxxix, 144 (1913); Craib, *ibid.*, xxxix, 186, fig. 88 (1913); W. W. Sm. and Forrest, *ibid.*, liv, 17 (1929); Adamson, *ibid.*, liv, 79 (1929); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 20 (1928); Farrer, Engl. Rock Gard., ii, 133 (1919); The Garden, lxxxvii, 208 (1923); Ward in Gard. Chron., lxxxviii, 8 (1930); Bruun, Cytological Studies in Primula, 24, 125 (1932). *P. humicola* Balf. f. and Forrest in Notes Roy. Bot. Gard. Edin., xiii, 10 (1920); Hand.-Mzt. in Symb. Sin., vii, 734 (1936), and in Journ. Roy. Hort. Soc., liv, 61 (1929). *P. heucherifolia* subsp. *humicola* (Balf. f. et Forrest) W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 20 (1928), and in Journ. Roy. Hort. Soc., liv, 17 (1929); Gould, *ibid.*, liv, 71 (1929).

This species was described by Hooker from material collected in the Chumbi valley which is in a corner of Tibet lying between Sikkim and Bhutan. The plant flowered at Kew in 1887 and was figured (Bot. Mag., *l.c.*). All the early records come from the Chumbi

valley and represent the work of native collectors in the employ of the Calcutta Botanic Garden, chiefly in 1877–1882. Even in 1905 (Pax, *l.c.*) the known distribution was confined to Chumbi and the much wider area quoted below is based on the collections of the last forty years. The species is usually found in forests and among shady boulders at 3000–4000 m. It is hardy in culture and reasonably well established.

In the original diagnosis Hooker associated the plant with *P. cortusoides* and in the Botanical Magazine (*l.c.*) called attention to a degree of variability in the foliage. This is also commented on by Pax (*l.c.*) who doubts whether the figure is in harmony with Hooker's description and with the dried material. But whether the drawing is imperfect or not, it can represent only *P. geraniifolia*. In 1913 the species was placed by Balfour (*l.c.*) along with *P. heucherifolia* and *P. septemloba* in his section Geranioides and thus not so near to *P. cortusoides*. This may well be agreed to, but as Geranioides is now included within section Cortusoides as a subsection, the difference cannot be stressed, based as it is mainly on leaf-form. Finally, the cytological evidence (Bruun, *l.c.*) is in favour of associating together *P. heucherifolia*, *P. geraniifolia*, and *P. latisecta*, keeping *P. septemloba* a little away, and *P. cortusoides* a little further! *P. geraniifolia* and *P. heucherifolia* differ in the lobing of their leaves and also in their distribution. *P. septemloba* and *P. geraniifolia* are readily confused, and their geographical areas touch but do not overlap. *P. septemloba* has larger leaves, monomorphic flowers and a different number of chromosomes in the cell nuclei. *P. geraniifolia* is chiefly Himalayan and Tibetan and just touches the Chinese frontier, while *P. septemloba* is predominantly Chinese. *P. humicola* (*l.c.*), regarded as a subspecies of *P. heucherifolia* by Smith and Forrest (*l.c.*), is in this review included within *P. geraniifolia*—a transference more in accord with its flower-structure as well as with its geographical distribution.

A hairy perennial with a slender more or less creeping rootstock. Leaves including the petiole 5–20 cm. long; lamina 3–8 cm. long and broad, orbicular in outline, deeply cordate at the base, palmately and acutely 7–9-lobed, the lobes deeply or shallowly dentate, dark green and thinly covered with septate hairs above, paler green with long outward spreading hairs on the nerves below, or more or less scabrid with shorter hairs; midrib and 2–3 pairs of basal or subbasal lateral nerves slightly sunk above, prominent below; reticulation very wide and poorly developed; petiole 4–13 cm. long, very conspicuously covered with long articulate pale tawny hairs.

Scape 10–30 cm. long, slender, pilose, carrying an umbel of 3–12 semipendent flowers or occasionally two superposed umbels; bracts 5–8 mm. long, linear or lanceolate to narrowly oblong, slightly hairy; pedicels 5–15 mm. long, minutely puberulous, at fruiting time up to 4 cm. long, stiff and erect. Calyx 5–10 mm. long, campanulate, often stained deep dull reddish-brown, cut to the middle into lanceolate teeth each with one prominent main nerve and often with two subprominent lateral nerves. Corolla rose to purple, annulate or exannulate, heteromorphic; tube 1–2 times the length of calyx, cylindrical, ampliate above insertion of stamens; limb 1–2 cm. in diameter with obcordate faintly or obviously emarginate lobes. Stamens, with anthers 1.5 mm. long, inserted at apex of corolla-tube in thrum-eyed flowers, near middle or a little lower in pin-eyed. Long style as long as corolla-tube; short style about half length of tube. Capsule as long as or a little longer than calyx, dehiscent by longitudinal valves. Seeds 0.75–1 mm. in diameter, quadrate-angular or ovoid, vesicular-areolate.

P. geraniifolia is represented in the Edinburgh Herbarium by the following collections:—

SIKKIM: Dikchu (*W. W. Smith*, 3721); Kanglasa (*Cave* in 1916); Karponang (*Cave* in 1917); Karponang and Laghep (*Cooper*, 563); below Changu (*Ribu*, 7422).

NEPAL: Tambakhane (*Sharma*, 335); Takar (*S.* 487).

BHUTAN: Parshong, Timpu (*Cooper*, 2585); Dotena, Timpu (*C.* 3896); Leo La, Ritang (*Ludlow and Sherrieff*, 3173); Tsalimape (*Gould*, 921); La ree (*Dungboo*, 196); sine loc. (*J. C. White*).

S. TIBET: Chumbi, Galing, between Chumbi and Phari (*Dungboo* in 1882; *Rhomoo Lepcha*, 62); Rinchigong (*King's Collector*, 4256—*co-type*); Pey-goong la (*King's Collector*, 448).

S.E. TIBET: Mt. Kenichumpo, Salwin-Irrawady divide (*Rock*, 21949); Tsarong, on Ka-gwr-pu, Mekong-Salwin divide (*Forrest*, 14236—*type* of *P. humicola*).

YUNNAN: Si-la, between Mekong and Salwin Rivers (*Hand.-Mzt.*, 8945); Salwin-Mekong divide (*Ward*, 88).

P. heucherifolia Franch. in Bull. Soc. Bot. Fr., xxxiii, 65 (1886), and in Nouv. Arch. Mus. Hist. Nat. Paris, ii, 93 (1887); Pax in Engl. Bot. Jahrb., x, 169 (1889); Diels, *ibid.*, xxix, 520 (1900); Pax in Engl. Pflanzenr. Primulaceae, 30 (1905); Forbes and Hemsl. in Journ. Linn. Soc., xxxvi, 504 (1905); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 134, 144 (1913); W. W. Sm. and Forrest, *ibid.*, liv, 17 (1929); Gould, *ibid.*, liv,

71 (1929); Adamson, *ibid.*, liv, 79 (1929); *ibid.*, liv, Proc., p. lv (1929); The Garden, lxxxvii, 208 (1923); Farrer, Engl. Rock Garden, ii, 139 (1929); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 20 (1928); Bruun, Cytological Studies in Primula, 24, 125 (1932); Cowan in Bot. Mag., t. 8908 (1938). *P. Gagnepainii* Petitm. in Bull. Herb. Boiss., vii, 964, f. 4 (1907); Gard. Chron., l, 102, fig. 47 (1911). *P. lanata* Pax et K. Hoffm. in Fedde Repert., xvii, 93 (1921); Hand.-Mzt. in Medd. Göt. Bot. Trad., ii, 110 (1926); *P. oculata* Duthie mss. in Herb. Kew (anno 1906); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 135, 144 (1913).

This species was first collected in 1869 by Abbé David in the district of Moupin, at that time regarded as in Eastern Tibet, but nowadays ascribed to Western Szechwan. It is not yet known to occur outwith the latter province and is found there at 2000–3200 m. in grassy places, in the shade of rocks, and occasionally in woods. In his first diagnosis Franchet associated it with *P. septemloba*, and in his second statement (*l.c.*, 93) he quoted also as possible allies *P. geraniifolia* and *P. mollis*. Little divergence from this point of view need be expressed, but it may be mentioned here that the cytological data according to Bruun (*l.c.*, 24, 125) indicate that *P. geraniifolia* and *P. latisecta* come nearest.

The literature concerning this species and its synonyms contains several inaccuracies which should be referred to in the sequence of their occurrence. Franchet's specific name was written *heucheraefolia*, but all subsequent commentators have used the amended form. The original material of David was doubtless meagre in quantity, for apparently no duplicates were distributed from Paris and it was a long time before the specimens of other collectors were recognised as *P. heucherifolia*. Thus, material collected by Faber, by Henry, and by Pratt in the period 1887–1890 was not named until much later (about 1913). Consequently in 1905 Pax in his Monograph (*l.c.*, 30) had little to report under the species, and what is reported is by some mischance incorrectly stated. He attributes the discovery of the plant at Moupin to Delavay, and the only other citation for the species is based on a Delavay specimen from a place in Yunnan where Delavay certainly obtained *P. septemloba*, but not David's plant. But just at the time of the Monograph and unfortunately too late for incorporation came the collections of E. H. Wilson who was exploring in Szechwan in 1904. His specimens and seeds secured in that year were forwarded to Messrs. Veitch & Sons. The dried material under Wilson 4054 was gifted in part to

Kew, but one sheet went to Paris. Let us deal with that sheet now, for it was not equated by Petitmengin in Paris with *P. heucherifolia* but became his type of *P. Gagnepainii* (*l.c.*). Petitmengin states that the number is Wilson 4034 (it should be 4054); he states that the locality is unreadable; it is Tatsienlu. The name, however, persisted for some time (*Gard. Chron., l.c.*); it is related that Wilson sent seeds to Miss Willmott and the resulting plants were named and figured as *P. Gagnepainii*. A correction was not made until Balfour (*l.c.*, 144) in 1913 stated concisely that the name was synonymous with *P. heucherifolia*. The Wilson specimens received at Kew and the seeds sown by Messrs. Veitch took another course. Flowering plants for the first time were produced in this country in 1906 (not 1904 as quoted by Balfour (*l.c.*, 144) and by Cowan (*l.c.*)). The flowering plants were named by Duthie *P. oculata*, but there is no evidence that this name was published although it was current in gardens for the Wilson plant. The specimen on which the name is based is in the Kew Herbarium with a ticket written up in Duthie's handwriting quoting Wilson as the collector in 1904 and stating that the specimen itself came from Hort. Veitch in 1906. Also in Duthie's handwriting is the number Wilson 4054. There was no suggestion at the time that this specimen had anything to do with *P. heucherifolia*, nor was it equated with Petitmengin's species, possibly because of the incorrect citation of the number by the French author. Consequently, even at the Primula Conference of 1913, *P. oculata* (Balfour, *l.c.*, 144) is quoted but not as a synonym. In 1928 the type of *P. heucherifolia* was on loan to Edinburgh and *P. oculata* was seen to be equivalent to it. The species was figured in the Bot. Mag. (*l.c.*) in 1938, but the text accompanying the figure errs in quoting a figure of Franchet and in stating that Forrest sent seed home in 1906. What he sent was *P. septemloba*. In 1928 Smith and Forrest (*l.c.*) were able to compare notes with Dr. Handel-Mazzetti regarding the validity of *P. lanata*, which proved to be another synonym. Finally, *P. humicola* is quoted in error as a subspecies of *P. heucherifolia* by Smith and Forrest (*l.c.*); the former plant must be placed under *P. geraniifolia* (*q.v.*). *P. heucherifolia* continued in cultivation after its introduction by Wilson, survived in Edinburgh until 1940 and may still persist elsewhere in the country.

A hairy stoloniferous perennial with a slender creeping rhizome. Leaves including the petiole 6–15 cm. long; lamina 3–7 cm. long, 3–6 cm. broad, orbicular in outline, deeply cordate at the base, palmately 7–11-lobed, the lobes ovate-deltoid irregularly and

bluntly dentate, dark green with a thin covering of long hairs above, lighter green below and thickly pilose on the nerves, the hairs multiseptate and outward spreading, elsewhere covered with white or brown sessile glands; nerves rather impressed above; midrib and 3 pairs of basal or subbasal lateral nerves prominent below; reticulation open; petiole 3–10 cm. long, thickly coated with pale tawny hairs. Scape 15–30 cm. long, hirsute-pubescent, slender, thickening at fruiting-time, carrying an umbel of 3–10 nodding flowers; bracts 5–7 mm. long, linear-lanceolate, puberulous; pedicels 1–3 cm. long, slender, shortly hairy, suberect at fruiting time. Calyx 4–7 mm. long, campanulate, puberulous and with a few long hairs on the outside, cut to the middle or a little lower into lanceolate to triangular-ovate apiculate lobes, each with one prominent nerve and often a pair of strong lateral nerves. Corolla mauve-pink to a rich deep purple, exannulate but with variously coloured concentric rings at the throat, heteromorphic; tube usually about twice the length of calyx, sometimes only a little longer, cylindrical, ampliate above insertion of stamens; limb 1–2.5 cm. in diameter with obcordate emarginate lobes. Stamens, with anthers 1 mm. long, inserted near base of corolla-tube in pin-eyed flowers, almost at mouth of tube in thrum-eyed. Long style as long as corolla-tube or slightly exserted; short style 1–2 mm. long. Capsule subglobose, shorter than calyx, dehiscing by longitudinal valves. Seeds 0.75 mm. in diameter, ovoid or irregularly quadrate, vesicular-surfaced.

The species is represented in the Edinburgh Herbarium by the following collections:—

SZECHWAN: Moupin (*Wilson*, 1165); Wa-Shan (*W.* 3158); Tatsienlu (*W.* 4054); Pao-hsieng Hsien (*Yü*, 1921, 2192); Ya Chou fu (*Limpricht*, 1605—*co-type* of *P. lanata*); photo. *David* in 1869—*type* in Herb. Paris; photo. *P. oculata* Duthie mss. in Herb. Kew (presumably *Wilson* seed under 4054).

P. jesoana Miq. in *Ann. Mus. Bot. Lugd.-Bat.*, iii, 119 (1867), and *Prol. Fl. Jap.*, 283 (1867); Franch. and Savatier, *Enum. Pl. Jap.*, i, 299 (1875); Pax in *Engl. Bot. Jahrb.*, x, 170 (1889), and in *Engl. Pflanzenur. Primulaceae*, 32 (1905); Matsumura, *Ind. Pl. Jap.*, ii, 2, 480 (1912); Takeda in *Notes Roy. Bot. Gard. Edin.*, viii, 86, pl. xv (1913); Miyoshi and Makino, *Pocket Atlas, Alp. Pl. Jap.*, i, t. xxvii, fig. 155 (1913); Balf. f. in *Journ. Roy. Hort. Soc.*, xxxix, 144, 175–77 (1913); Makino and Nemoto, *Fl. Jap.*, 388 (1925); *Journ. Jap. Bot.*, iii, No. 10,

t. 3 (1926); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 20 (1928), and in Journ. Roy. Hort. Soc., liv, 17 (1929); Report Nat. Monuments Invest. Plants, No. 11, pl. 2 (1930); Cooper in New Fl. and Silva, v, 266, 270, fig. xci (1933); Kitagawa in Tokyo Bot. Mag. 1, 196 (1936); Hara, *ibid.*, 1, 569 (1936); Takeda, Alp. Flowers Japan, fig. 75 (1938). *P. jesoana* f. *pubescens* Takeda in Notes Roy. Bot. Gard. Edin., viii, 86 (1913)—in nota, excl. pl. Quelpaert; Tatewaki, Veg. Apoi, 105 (1928); Nakai, Veg. Apoi, 65 (1930). *P. jesoana* f. *glabra* Takeda in Notes Roy. Bot. Gard. Edin., viii, 86 (1913); Tatewaki, Veg. Apoi, 105 (1928). *P. jesoana* f. *nudiuscula* (Naka et Kitagawa) Hara in Tokyo Bot. Mag., 1, 569 (1936). *P. jesoana* var. *pubescens* (Takeda) Takeda and Hara in Tokyo Bot. Mag., 1, 569 (1936). *P. jesoana* var. *glabra* (Takeda) Takeda and Hara in Tokyo Bot. Mag., 1, 569 (1936). *P. jesoana* var. *pubescens* f. *albiflora* Tatewaki, Veg. Apoi, 105, 131 (1928). *P. jesoana* var. *glabra* f. *leucantha* Hara in Tokyo Bot. Mag., 1, 569 (1936). *P. yesomontana* Nakai and Kitagawa in Tokyo Bot. Mag., 1, 140 (1936). *P. yesomontana* var. *nudiuscula* Nakai and Kitagawa in Tokyo Bot. Mag., 1, 141, fig. 9 (1936). *P. hondoensis* Nakai and Kitagawa in Tokyo Bot. Mag., 1, 139, fig. 8 (1936). *P. yedoensis* Franch. and Savatier, Enum. Pl. Jap., ii, 429 (1879). *P. yesoana* Petitm. in Bull. Herb. Boiss., vii, 532 (1907).

This Japanese species was described by Miquel in 1867 along with *P. kisoana*. The original specimens were obtained in Yezo and according to Miquel by a Japanese botanist whose name was possibly Sugerok. In Miquel's description no affinity is suggested for *P. jesoana*. In 1905 this species along with *P. kisoana* was placed by Pax in his section Fallaces. It does not appear that Pax had any material of either species, and the reasons against associating these two plants with *P. Reinii* are dealt with by Takeda (*l.c.*) and also under *P. kisoana*. In the same paper of Takeda *P. jesoana* is divided into two forms (later called vars.), form *glabra* and form *pubescens*. Takeda gives the distribution as Yezo and mountainous districts of Central Japan, and also includes Korea and the island of Quelpart. This opinion, however, as will be seen, he subsequently modifies and restricts the distribution to Japan (*l.c.*, 569). [The Korean and Quelpart plant will be referred to under *P. Loeseneri*.] Takeda placed the species near *P. septemloba* and *P. geranii-folia*, and this is also the view taken in 1913 at the Primula Conference by Balfour (*l.c.*) who has it in his section Geranioides

It was, however, at that time not in cultivation in this country. Living plants in the resting condition were secured from Japan in 1932, came into flower at Edinburgh and still persist. A figure is given of the cultivated plant by Cooper (*l.c.*).

Some further notes by Takeda, including a figure, are available in his book entitled "Alpine Flowers of Japan" (*l.c.*). Between his first paper and this second reference by him to *P. jesoana* some additional names had been given to varieties and forms of this species as will be evident from the literature cited. These appear to be of a trivial nature for they are differentiated from *P. jesoana* by very slender and in our view quite unsatisfactory characters. Thus *P. hondoensis* and *P. yesomontana* cited above in the literature are both referred to in Takeda's book and reduced to one or other of his own two varieties, *glabra* and *pubescens*. It is possible that *P. hallaisanensis* described from the island of Quelpart comes also very near *P. jesoana*, but is perhaps better ascribed to *P. Loeseneri* as indistinguishable from that plant.

Although it is stated above that the association of this species is with *P. geraniifolia* and *P. septemloba*, it is certain that *P. Loeseneri* is very much more closely allied, if indeed it can be clearly discriminated from it. The two species have been already much mixed in literature, and separation depends partly on the geography and to some extent on the shape of the leaf. Plants in Korea and in Quelpart formerly associated with *P. jesoana* are now relegated to *P. Loeseneri*, and this confusion even in good authorities is a clear indication that the two are separable only with difficulty.

The material of this species available in herbaria is scanty. Several sheets collected by Faurie in Japan and now in Herb. Kew have been particularly serviceable. Takeda calls the capsule globose, but these Faurie sheets show also elongate capsules which may be shorter than the calyx, equal to it, or exceeding it. The size of the seeds is given by Nakai and Kitagawa (*l.c.*, 141), but their measurements are much in excess of anything known for any species in subsection Geranioides. The figures quoted in the following description are based upon seeds examined in Edinburgh.

A hairy or almost glabrous perennial with a short rhizome. Leaves including the petiole 10-35 cm. long; lamina 2-10.5 cm. long, 2-12 cm. broad, in outline $\pm$ orbicular, deeply or rarely shallowly cordate at the base, palmately 7-9-lobed, the lobes lobulate and irregularly dentate to incised-dentate, dark green and almost glabrous above or thinly covered with septate hairs,

paler below and either glabrous or with hairs along the veins; midrib and 3-4 pairs of basal or subbasal lateral nerves rather impressed above, prominent below; petiole 7-30 cm. long, slender, glabrous or quite densely pilose. Scape 10-60 cm. long, slender, glabrous except towards the apex which is markedly puberulous or even pilose, carrying 1-4 umbels each with 2-6 flowers; bracts 4-10 mm. long, narrowly linear to lanceolate or oblong, glabrous without, puberulous within, with one prominent nerve; pedicels 3-10 mm. long, in fruit up to 33 mm. long, puberulous or pubescent. Calyx 4.5-10 mm. long, tubular to tubular-campanulate, markedly puberulous, sometimes almost glabrous, cut to below the middle into lanceolate or linear-lanceolate acute or obtuse mucronulate lobes each with 3 nerves. Corolla rose or rose-purple, sometimes white, with a yellow eye, slightly annulate, heteromorphic; tube 1-2 times, usually 2 times, the calyx, cylindrical, ampliate above the insertion of stamens; limb 1-2 cm. in diameter with obcordate emarginate lobes. Stamens, with anthers about 1.5 mm. long, inserted at the apex of the corolla-tube, reaching the annulus in thrum-eyed flowers, in the lower half of the tube in pin-eyed. Long style as long as corolla-tube, short style about 3 mm. long. Capsule globose or ellipsoid, shorter than, as long as, or longer than the calyx, dehiscing by longitudinal valves. Seeds 1-1.5 mm. in diameter, flattened, ovoid to quadrate, vesicular-surfaced.

Represented in the Edinburgh Herbarium by the following collection:—

JAPAN: Sinano Province, on Mount Sirouma (*Takeda* in 1905); spec. cult. in Hort. Edin.; photo. of plant cult. in Hort. Edin.

- P. kisoana** Miq. in Ann. Mus. Bot. Lugd. Bot., iii, 119, et Prolus. Fl. Jap., 283 (1867); Somoku Dzusetsu, Ed. 2, iii, t. 22 (1874), Ed. 3 (Makino), iii, t. 22 (1907); Franch. and Savatier, Enum. Fl. Jap., i, 299 (1875); Pax in Engl. Bot. Jahrb., x, 170 (1889), and in Engl. Pflanzenr. Primulaceae, 32 (1905); Franch. in Bull. Soc. Philom. Paris, xii, 93 (1888); Makino in Tokyo Bot. Mag., viii, 173 (1894); Useful Pl. Japan, iii, t. 902 (1895); Matsumura, Index Pl. Jap., ii, 2, p. 480 (1912); Takeda in Notes Roy. Bot. Gard. Edin., viii, 86, pl. xvi (1914); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 175-7 (1913); W. W. Sm. and Forrest, *ibid.*, liv, 17 (1929); *ibid.*, lix, Proc., p. clxviii (1934); *ibid.*, lxiii, 295, Proc., p. lxxiii (1938); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 20 (1928); Cooper in New Fl. and Silva, v, 266, 270 (1933);

Stapf in Bot. Mag., t. 8884 (1938). *P. kisoana* var. *shikokiana* Makino in Journ. Jap. Bot., No. 6, 19 (1917). *P. tosaensis* Hort. in Journ. Roy. Hort. Soc., liv, figs. 4, 5 (1929)—nec Yatabe. *P. hirsuta* Siebold in sched. ex Miquel—nec All.

According to Takeda (*l.c.*, 86) *P. kisoana* is one of the most beautiful, interesting and rare of the Japanese Primulas and was in cultivation in Japanese gardens two centuries ago. It was figured and described in a Japanese book of gardening in 1733 under a vernacular name "katsu-kô-sô," which means "super-crimson (or deep rose) flower." The finding of the type in Kiso over one hundred years ago is attributed to the Japanese botanist Ito Keiske, but no more specimens have since been recorded from that particular locality. Its distribution is confined to S.W. Japan where it is secured only very occasionally. In his original diagnosis based on a single incomplete specimen Miquel (*l.c.*) associates the species with *P. cortusoides*. This placing, which is reasonably near the mark, was departed from in 1889 by Pax (*l.c.*) and again in 1905 in his Monograph (*l.c.*, 32), where *P. kisoana* is assigned to his section Fallaces in company with *P. Reinii* and *P. tosaensis*. That these views of Pax were quite mistaken is clearly demonstrated by Takeda (*l.c.*) who advocates relationship with *P. jesoana* and *P. mollis*. Stapf's opinion, given in Bot. Mag. (*l.c.*), favours *P. jesoana* as nearest of kin and in this we concur. The earliest record of cultivation in this country appears to be in the years 1916-18 at Edinburgh, and after an interval again in 1934-43 when it was lost. Plants exhibited by Lord Aberconway in April 1934 received an Award of Merit (Journ. Roy. Hort. Soc., lix, *l.c.*). Plants in culture did not set seed and propagation was slow and uncertain.

A very hairy perennial with a short rhizome. Leaves 3-7 in a tuft, 5-15 cm. long including the petiole; lamina 2.5-7 cm. long and broad, orbicular in outline, deeply cordate at the base, shallowly or obscurely lobulate at the margin, with the lobules broadly and often indistinctly crenate, or the margin merely wavy, thinly covered above with long white septate hairs, very densely below or only along the main nerves with similar hairs; midrib and 2-3 pairs of basal or subbasal lateral nerves slightly impressed above, prominent below; petiole 2.5-10 cm. long, more or less fleshy, often reddish-tinted, usually thickly covered with long pinkish articulated hairs. Scape 5-20 cm. tall, sturdy and erect, hairy like the petioles, carrying an umbel of 2-6 flowers or occasionally two superposed umbels; bracts 5-6 mm. long, linear to lanceolate, pilose; pedicels 5-30 mm. long, pilose. Calyx 8-12 mm. long, campanulate to

tubular-campanulate, densely pinkish villous, cut to beyond the middle into lanceolate acute slightly spreading lobes, each usually with one prominent nerve. Corolla deep rose or rose-mauve, red in the tube, annulate, heteromorphic; tube about twice as long as calyx, cylindrical, ampliate above insertion of stamens, villous on the outside and pubescent within; limb 2.5–3 cm. in diameter with obcordate-oblong deeply emarginate lobes. Stamens, with anthers nearly 2 mm. long, inserted at middle of corolla-tube or slightly above in pin-eyed flowers; at apex of tube, reaching annulus in thrum-eyed. Long style prominently exerted beyond annulus; short style about half the length of corolla-tube. Capsule subglobose, as long as calyx, dehiscing by longitudinal valves. Seeds. . . .

This species is represented in the Edinburgh Herbarium by the following specimens:—

JAPAN: Sikok, Iyo, Kamomura (*Yamamoto* in 1929); sine loc. (*Mochizuki* in 1910); spec. exsicc. (cult. Bot. Gard. Edin. in 1935).

P. latisecta W. W. Sm. in Notes Roy. Bot. Gard. Edin., xv, 74 (1926); W. W. Sm. and Forrest, *ibid.*, xvi, 20 (1928); Ward in Journ. Roy. Hort. Soc., lii, 23 (1927); W. W. Sm. and Forrest, *ibid.*, liv, 17, fig. 57 (1929); Gould, *ibid.*, liv, 71 (1929); *ibid.*, lvii, Proc. p. xxv (1932); Gould, *ibid.*, lxi, 256 (1936); Stapf in Bot. Mag., t. 9245 (1931); Bruun, Cytological Studies in *Primula*, 24, 26, 28, 125 (1932).

P. latisecta was discovered by Ward in 1924 on the Nyima La in S.E. Tibet at about 4000 m., growing in the forest under heavy shade. The only other collections were made in 1938 by Ludlow, Sherriff and Taylor who record it as occurring in great numbers on the right bank of the Drukla Chu, near the south shore of the Pasum Lake, on the Tongyuh River east of the Nambu La and below Pangkar. The nearest ally is probably *P. palmata* which has leaves more deeply cut with the ultimate segments more or less acute. In *P. latisecta* the obovate leaf-lobes are separated by wide rounded sinuses. Certainly also akin are *P. geraniifolia* and *P. septemloba*. From the purely cytological point of view Bruun (*l.c.*) associates it with *P. geraniifolia* and *P. heucherifolia*, but not with *P. septemloba*. The species was successfully introduced into cultivation from seeds collected by Ward, flowered in 1927 and still persists.

A hairy perennial with a slender creeping rhizome. Leaves 2–4 in a tuft, including the petiole 8–18 cm. long; lamina 4–6 cm. long, 4–8 cm. broad, orbicular to suborbicular in outline, deeply cordate

at the base, palmately divided to the middle into 7 obovate lobes each more or less trilobulate and slightly toothed and with the sinuses between the lobes always rounded, dark green and lightly covered with long articulated hairs above, paler green with similar but more numerous hairs below especially along the veins, and with small round sessile glands; midrib and 3 pairs of basal or subbasal lateral nerves prominent on the lower surface; petiole 5–14 cm. long, not vaginate at the base, thickly covered with very long pale tawny multiseptate hairs. Scape 7–20 cm. long, slender, slightly thickening at fruiting time, sparsely pilose, carrying an umbel of 2–4 flowers; bracts 4–8 mm. long, linear-lanceolate, sparsely pilose; pedicels 10–15 mm. long, erect, pilose. Calyx 7–10 mm. long, campanulate, pubescent or subglabrous, divided to the middle or a little lower into narrowly lanceolate acuminate lobes, ciliate at the margin, slightly recurved at the apex, with one prominent main nerve and two subprominent lateral nerves. Corolla rose or purplish with a white or pale yellow eye, annulate, heteromorphic; tube $1\frac{1}{2}$ –2 times the length of calyx, cylindrical, ampliate above insertion of stamens; limb 2–2.5 cm. in diameter, with obcordate deeply emarginate lobes, sometimes with a tooth in the sinus. Stamens, with anthers about 1 mm. long, inserted at base of corolla-tube in pin-eyed flowers, almost reaching annulus in thrum-eyed. Long style reaching annulus; short style 2–3 mm. long. Capsule more or less oblong, not quite as long as calyx, dehiscing by longitudinal valves. Seeds 0.75–1 mm. in diameter, rounded or ovoid, somewhat flattened, minutely areolate.

The type is in the Kew Herbarium and at Edinburgh are the following:—

S.E. TIBET: Nyima La (*Ward*, 5819—*co-type*); below Pangkar (*Ludlow, Sherriff and Taylor*, 6924); sine loc. (*L., S. and T.*, 5144, 5144a).

P. Loeseneri Kitagawa in *Tokyo Bot. Mag.*, 1, 137, 196 (1936), and in *Lineamenta Fl. Manshuricae*, 353 (1939). *P. Paxiana* (non O. Kuntze) Gilg in *Engl. Bot. Jahrb.*, xxxiv, Beibl. No. 75, 56 (1904); Pax in *Engl. Pflanzenr. Primulaceae*, 30, fig. 17 (1905); Balf. f. in *Journ. Roy. Hort. Soc.*, xxxix, 136, 146 (1913); Yabe, *Prel. Rep. Fl. Tsing-tau Reg.*, 89 (1919); *Icon. Fl. Manch.*, 1, 2, t. 15 (1920); Loesener, *Prodr. Fl. Tsingt.* in *Beih. Bot. Centralbl.*, xxxii, 165, t. 8, f. D–E (1919); W. W. Sm. and Forrest in *Journ. Roy. Hort. Soc.*, liv, 17 (1929); *Hand.-Mzt.*, *ibid.*, liv, 52 (1929); W. W. Sm. and

Forrest in Notes Roy. Bot. Gard. Edin., xvi, 20 (1928); Sato, Wild Flowers Manchuria and Mongolia, 86–87 (1927). *P. tyoseniana* Nakai ex Kitagawa in Tokyo Bot. Mag., 1, 137, fig. 7 (1936). *P. jesoana* (non Miquel) Nakai in Journ. Coll. Sc. Imp. Univ. Tokyo, xxxi, 78 (1911); Takeda in Notes Roy. Bot. Gard. Edin., viii, 86 (1913)—*pro parte*; Rep. Veg. Mt. Chiisan, 42 (1915); Rep. Veg. Diamond Mount, 182 (1918); Mori Enum. Pl. Cor., 283 (1922)—*pro parte*. ? *P. Maclareni* Balf. f. in Trans. and Proc. Bot. Soc. Edin., xxvii, 238 (1919); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 20 (1928), and in Journ. Roy. Hort. Soc., liv, 17 (1929); Bruun, Cytological Studies in Primula, 24, 125 (1932). *P. hallaisanensis* Nakai ex Kitagawa in Tokyo Bot. Mag., 1, 194, 197, fig. 10 (1936).

The above title was given by Kitagawa to a species which passed under another name (*P. Paxiana*) for over thirty years. Kitagawa described at the same time *P. tyoseniana*, using a ms. name given by Nakai to a plant from Manchuria and Korea. It is evident from the description that the two are very similar, and three years later Kitagawa himself (*l.c.*, 353) reduced *P. tyoseniana* to *P. Loeseneri*.

For the first description therefore of the plant now known as *P. Loeseneri* it is necessary to go back to Gilg (*l.c.*) who gave in 1904 the diagnosis of *P. Paxiana*. His type specimen in Herb. Berol. (and consequently the type specimen of *P. Loeseneri*) is Zimmermann 346 collected at 300 m. on Mt. Lao-shan at Kiaochow in the province of Shantung. According to Zimmermann the plant grew on wet grassy mountain slopes between stones and was rare. Gilg suggested no affinity, but in the following year Pax included the species in his Monograph and placed it between *P. geraniifolia* and *P. septemloba*, which is sufficiently accurate. The nearest species without doubt is *P. jesoana*, but Pax without material of the latter had relegated it to a separate section (Fallaces). Pax's quotation of 336 is apparently in error for the original 346.

In 1919 Yabe (*l.c.*) suggested that a Korean record for *P. jesoana* given by Nakai (*l.c.*) and referred to by Takeda (*l.c.*) should be referred to *P. Paxiana*, thus implying that *P. jesoana* should be confined to Japan and indicating the close proximity of the two species. A fifth name now comes into the problem. In 1919 Balfour (*l.c.*) described *P. Maclareni* which had been collected in 1915 at 1300 m. in Korea. His diagnosis indicates that he included it in his section Geranioides and associated it with

P. septemloba and also with *P. jesoana*. No dried material from Korea was ever available to him and the diagnosis was based on plants grown from Korean seed. A similar plant was grown in Denmark by Mr. Olsen from seed collected on the banks of the Yalu River between Manchuria and Korea. Only lately has doubt arisen as to the validity of *P. Maclareni* as a distinct species. Comparison between it and living plants of *P. jesoana* indicated a near approach, and now it is almost certainly identical with *P. Loeseneri*.

The problem thus centres in the distinction between *P. jesoana* and *P. Loeseneri*. Both may be glabrous or subglabrous and both may be markedly pubescent or pilose. From a review of the literature and of the material at Kew and Edinburgh it is concluded that the distinctions between them do not amount to more than a difference in distribution and a difference (not too well defined) in the form of the leaf. It may be that the geographical difference is a valid one, but so easy a criterion tends to relegate all Japanese specimens to *P. jesoana* and all Continental specimens to *P. Loeseneri*—without any clear citation of morphological differences. Germane to this question is another series of names. Comparatively recently described and closely connected with *P. jesoana* and therefore with *P. Loeseneri* are the following: *P. hondoensis*, *P. yesomontana*, and *P. hallaisanensis*. From the descriptions given and from the statements made with regard to them by Japanese botanists subsequent to the descriptions, it appears to be quite clear that they must be of the nature of microspecies or simply forms. Thus *P. hondoensis* and *P. yesomontana* have already been reduced (see under *P. jesoana*). There remains *P. hallaisanensis*, and in our view it also should be reduced, but whether it should go to *P. jesoana* or to *P. Loeseneri* is difficult to decide as the differences between these two species appear to be of little moment. If the distribution is invoked then the plant goes to *P. Loeseneri*. It is true that there is a key available (Kitagawa, *l.c.*, 196) where most of these names are cited, but where the distinctions given are of such little weight that certain Japanese botanists have already reduced all the names except *P. hallaisanensis*, and we need concern ourselves only with it. This plant was at first recorded by Nakai (*l.c.*) and by Takeda (*l.c.*) as a pubescent form of *P. jesoana* but occurring in Quelpart. It has been figured (*l.c.*) but the figure is quite inconclusive; the seed measurements given for it appear excessive and await confirmation. It comes from Hallaisan, which is a locality cited also for *P. Loeseneri* and for the form of *P. jesoana* referred to above by Takeda. The evidence therefore points to its

being equivalent to *P. Loeseneri*—from the geography, from the description, and from the extreme tenuity of the discriminating characters cited.

The problem has therefore been simplified to the distinctions between *P. jesoana* and *P. Loeseneri*, as all other names can be more or less accounted for. As noted above, the distinctions are based on the geography and on the form of the leaf. Usually the leaves in *P. jesoana* are very deeply cordate and those of *P. Loeseneri* shallowly cordate. Those botanists, however, who have had an opportunity of comparing much more material of both than is available to us at present have not so far ventured to combine the two (if the earlier opinions of Nakai and Takeda are excluded), nor are we prepared as yet to solve the problem thus.

The name given by Gilg is invalidated by an earlier homonym of O. Kuntze (Rev. Gen., i (1891) 400) as is stated by Kitagawa (*l.c.*, 196). Pax in his Monograph (*l.c.*, 30) continued to use Gilg's binomial and also (*l.c.*, 174) quoted that of Kuntze. Subsequent references up to 1936 follow in the wake of Pax. But in its turn the type, *P. Loeseneri*, may have to yield for reasons of priority to *P. Maclareni*. The latter, however, is based on cultivated material and it is an open question whether it is not as referable to *P. jesoana* as to *P. Loeseneri*. In the circumstances we have not given the name *P. Maclareni* precedence over *P. Loeseneri*. We are inclined to suspect that *P. jesoana* is capable of including all the names discussed above under *P. Loeseneri* and *P. Loeseneri* itself.

A subglabrous or hairy perennial with a somewhat elongate rhizome producing ovoid perennating buds covered by a few reddish-brown membranous scales. Leaves including the petiole as much as 37 cm. long, lamina 5–12 cm. long, 6–17 cm. broad, reniform or suborbicular, cordate at the base with an open or closed sinus, shallowly 7–9-lobulate with the lobules triangular-deltoid and dentate to repand-dentate at the margin, bright green and more or less glabrous above, paler and glabrous or pubescent below; midrib and 3 or 4 pairs of basal or subbasal lateral nerves slightly impressed above, conspicuous below; reticulation open and poorly developed; petiole up to 30 cm. long, sparsely pilose. Scape 40–70 cm. tall, slender, subglabrous to densely pilose, bearing 1–4 superposed umbels each with 2–8 flowers; bracts 4–9 mm. long, linear-subulate; pedicels 3–12 mm. long, in fruit up to 20 mm. long, pubescent. Calyx 6–10 mm. long, campanulate, puberulous or papillose-punctate, cut almost to the base into lanceolate to triangular-lanceolate apiculate lobes each with one main and two

lateral nerves. Corolla rose to crimson-lake with a greenish or yellow eye, annulate, heteromorphic; tube 2-3 times the calyx, cylindrical, ampliate above insertion of stamens, glandular-puberulous without; limb 1.5-2 cm. in diameter with obcordate or almost orbicular emarginate lobes. Stamens, with anthers about 1.5 mm. long, inserted at apex of corolla-tube and touching the annulus in thrum-eyed flowers, towards base of tube in pin-eyed. Long style slightly exerted beyond annulus; short style as long as or shorter than the calyx. Capsule shorter than calyx, ellipsoid, dehiscing by longitudinal valves. Seeds. . . .

This species is no longer in culture in this country and is represented in the Edinburgh Herbarium by the following collections:—

KOREA and MANCHURIA: Hallaisan, Quelpart (*Faurie* in 1900); Diamond Mountain (*Faurie*, 741); cultivated specimens raised from seed collected in Manchuria; coloured drawing from plant cult. Hort. Edin.; coloured drawing from plant cult. Hort. Olsen.

P. Minkwitziae W. W. Sm. in Notes Roy. Bot. Gard. Edin., xviii, 181, pl. ccxlvii (1934). *Cortusa Matthioli* Podpéra (nec Linn.) in Beihefte Bot. Centralbl., xxxix, Abt. ii, 286 (1921-23).

Nothing as yet can be added to the original description. The type is a single sheet in the Vienna Herbarium to which Dr. Handel-Mazzetti directed our attention in 1934. This Vienna type is itself a duplicate from material under *Cortusa Matthioli* in the Leningrad Herbarium. The illustration accompanying the first diagnosis makes the position clear. The specimens were secured in 1908 by Madame Minkwitz in the Syr Darya region of Turkestan, in the district of Chinkent, on the screes of Mt. Dshebogli. The only other reference to the plant is in an article by Podpéra (*l.c.*, 286) who considers the solitary specimen available to him as possibly a form of *C. Matthioli*.

The nearest allies are possibly *P. palmata* and *P. alsophila*, from which, however, it differs widely in the shape of the leaf, in the usually entire lobes, in the solitary flower, and in the corolla being hairy without. There is no record of the plant in culture.

A sparingly pilose perennial beset at the base with the remains of withered petioles. Leaves apparently few for each plant, about 8 cm. long including the petiole; lamina 3-3.5 cm. in diameter, orbicular to reniform in outline, somewhat fleshy in texture, palmately divided for a third or a quarter into 7 lobes, the lobes broadly ovate or subquadrate entire and obtuse or trilobulate,

ciliolate at the margin with whitish pellucid hairs, cordate or subtruncate at the base, slightly scabrid above, sparsely pilose on the nerves below; midrib and 3 pairs of basal or subbasal lateral nerves prominent below; petiole 5-5.5 cm. long, well covered with septate hairs. Scape about 7 cm. long, pilose, 1-flowered; bracts 3-4 just below calyx, 3-6 mm. long, linear-lanceolate subacute densely and shortly hairy. Calyx about 7 mm. long, cylindrical, green, shortly hairy, cut to the middle into linear-lanceolate subacute teeth. Corolla probably purple; tube about 11 mm. long, 2 mm. broad, cylindrical, lightly covered without with white pellucid hairs; lobes of the limb about 6 mm. long, narrowly obovate, deeply emarginate.

Represented in the Edinburgh Herbarium by a photograph of the type:—

TURKESTAN: Syr Darya, in district Chimkent, N. of Tashkent (*Minkwitz*, 1189, in *Herb. Vienna*).

P. Normaniana Ward in *Ann. Bot.*, xliv, 123 (1930); Gould in *Journ. Roy. Hort. Soc.*, lxi, 256 (1936); Ward in *Quart. Bull. Alp. Gard. Soc.*, vi, 299 (1938); Sherriff and Taylor, *ibid.*, vii, 228, fig. p. 225 (1939).

This species was discovered by Ward in 1928 in the Assam Himalaya, growing by streams in the forest and forming large colonies on steep shady faces at 3300-3700 m. Subsequently its distribution was extended to an area in S.E. Tibet where it frequents shady damp banks in bamboo and mixed forest. Sherriff and Taylor (*l.c.*) record its occurrence through a wide altitudinal range between 2200 and 4000 m. As Ward points out in his diagnosis, its only near relations are *P. vaginata* and *P. eucyclia*. It agrees with these in its leaf form and particularly in the vaginal extension at the base of the petiole, but differs from both in the more robust habit, in the much congested inflorescence with short pedicels, and in the fimbriate corolla-lobes. Seeds secured by Ward gave rise at Edinburgh and elsewhere to flowering plants in 1931. The species is still in cultivation at this date but sparingly. The figure cited above shows *P. Normaniana* in its natural habitat.

A slightly pubescent or almost glabrous perennial with a stout or thin creeping rhizome. Leaves including the petiole 3-22 cm. long; lamina 1.5-8 cm. broad, 1.5-6 cm. long, orbicular, deeply cordate at the base, palmately cut into 7-9 lobes, the lobes lobulate or deeply and sharply dentate and the sinuses between the lobes rounded or bearing a distinct tooth, dark green and thinly covered

above with septate hairs which tend to wear away at maturity, pale green and glabrous below; midrib and 3-4 pairs of lateral nerves prominent below; reticulation $\pm$ obscure; petiole 2-18 cm. long, glabrous, markedly vaginate, membranous, 5-10 mm. broad for the basal 1-2 cm., sometimes reddish tinted. Scape 12-30 cm. tall, green or tinged with red, pubescent at the apex, sturdy and erect, carrying a compact head of 4-12 erect or suberect flowers; bracts 7-14 mm. long, ovate or elliptic to obovate or oblanceolate, foliaceous, entire or prominently toothed, ciliolate at the margin; pedicels 3-6 mm. long, pubescent. Calyx 5-8 mm. long, campanulate to tubular, broad at the base, cut to a third into ovate or orbicular often imbricate teeth, acute or rounded and apiculate at the apex, ciliate at the margin and with one prominent vein. Corolla bright purplish-pink with a yellow or crimson eye, annulate, heteromorphic; tube cylindrical, ampliate above insertion of stamens, 1-2 times the calyx; limb 1-1.5 cm. in diameter with obovate emarginate and usually fimbriate lobes. Stamens, with anthers 1 mm. long, inserted towards middle of corolla-tube in pin-eyed flowers, towards apex reaching or almost reaching annulus in thrum-eyed. Short style half the length of corolla-tube; long style exerted beyond annulus. Capsule shorter than calyx.

The type is in the Kew Herbarium and at Edinburgh are the following:—

ASSAM HIMALAYA: Mishmee Hills, Delei Valley (*Ward*, 8295—*co-type*, 8573).

S.E. TIBET: Lo La, Pachakshiri (*Ludlow and Sherriff*, 1903); (*Ludlow, Sherriff and Taylor*, 3650, 6574); Lhalung, Pachakshiri (*L., S. and T.*, 3700).

P. palmata Hand.-Mzt. in Anz. Akad. Wiss. Wien. Math.-Nat., 1924, lxi, 132 (1925), and in Acta Hort. Gothoburg., ii, 99, figs. 1 and 2 (1925-26); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 20 (1928), and in Journ. Roy. Hort. Soc., liv, 17 (1929).

This species was described from a single specimen collected by Dr. H. Weigold in 1914 on the mountains surrounding the town of Sungpan in N.W. Szechwan. The type in the Vienna Herbarium consists of one small plant with one complete flower and one without corolla. But the first to find the plant was E. H. Wilson in June 1908, as is indicated by *Wilson* 3151 in the herbaria of Kew and Edinburgh. He gives the colour of the flower as mauve-pink and the elevation as 2300-2700 m. The species is not known outside

Szechwan and is apparently far from common, for only two additional records can be cited. Handel-Mazzetti (*l.c.*, 99) was able to supplement his original description and to give figures from material collected in 1921-22 by Harry Smith at Dongrergo near Sungpan at 3900 m. (*H. Smith*, 3785, in Herb. Upsala). There is also in Herb. Fan Mem. Instit. Biology at Peking a good unicate sheet (which we have seen) under *F. T. Wang* 21214 from Pa-lang Shan, elevation 3600 m. The nearest ally is almost certainly *P. latisepta* which has a less divided leaf with the ultimate segments more rounded and a larger corolla. *P. vaginata* and its allies, also with much divided leaves, differ in the glabrous under-surface of the foliage and in the inflated petiolar base. There is no record of *P. palmata* in cultivation.

A slender hairy stoloniferous perennial with a thin creeping rhizome and with a few ovate membranous scales, 2-4 mm. long at the base. Leaves few, usually 1-4, including the petiole 2-27 cm. long; lamina 1-7.5 cm. in diameter, orbicular, palmately cut to three-quarters or more into 5-7 trilobulate lobes, the lobules 1-3-dentate, dark green and lightly covered with long septate hairs on the upper surface, pale green and with numerous long septate hairs on the veins below; midrib and 2-3 pairs of basal or subbasal lateral nerves prominent below; reticulation obscure; petiole 1-19 cm. long, thickly covered with long fulvous articulate hairs. Scape 4.5-17 cm. long, thinly covered with fulvous hairs, carrying an umbel of 1-3 flowers; bracts 3-5 mm. long, subulate, conspicuously hairy; pedicels 7-25 mm. long, erect, hairy. Calyx 5-7 mm. long, campanulate, pilose, cut almost to two-thirds into triangular to triangular-lanceolate trinerved lobes, membranaceous at the angles. Corolla rose to mauve-pink, annulate, heteromorphic; tube a little longer than the calyx or at least twice as long, narrowly cylindrical, ampliate above insertion of stamens; limb 1.5-2 cm. in diameter with obcordate emarginate undulate-crenate lobes. Stamens, with anthers 1.5 mm. long, inserted in upper part of corolla-tube in thrum-eyed flowers, near base of tube in pin-eyed. Long style as long as corolla-tube or even a little exserted; short style about 2 mm. long. Capsule and seeds not seen.

Represented in the Edinburgh Herbarium by the following specimen:—

W. SZECHWAN: Woodlands of Niu tou shan, west of Kuan Hsien (*Wilson*, 3151). Also photo. of *Weigold* type in Vienna Herb.

P. Pauliana W. W. Sm. et Forrest in Notes Roy. Bot. Gard. Edin., xiv, 51 (1923), in *ibid.*, xvi, 20 (1928), and in Journ. Roy. Hort. Soc., liv, 17, fig. 2 (1929); Forrest, *ibid.*, xlix, 34 (1924); W. W. Sm. in Trans. and Proc. Bot. Soc. Edin., xxix, 8, pl. 1 (1924); Bruun, Cytological Studies in Primula, 24, 26, 28, 125 (1932); Chen in Bull. Fan Inst. Biol., ix, 280 (1939).

This peculiar species was found by Forrest in 1922 on two occasions at 3700–4000 m. near Yungning, growing in open meadows or on the margins of thickets. The only other record is given by Chen (*l.c.*) in his enumeration of Primulas collected by Yü in 1937–38. The latter found it in the Muli district, between Huado and Nina at 3300 m. growing in shady rocky crevices. In the form and consistency of its leaves, in the numerous septate hairs, and in the lack of farina *P. Pauliana* is generally in accord with the other members of the subsection Geranioides, but differs from them somewhat widely in the racemose inflorescence occupying half the scape, in the yellow flowers, in the long curved capsule, and in the cytology. The sum of these divergences may well suggest a separate section for this one species, but its retention within Cortusoides can be defended. The lax raceme finds a parallel in certain species in the allied section Malvacea such as *P. blattariformis*. Similarly in the same section there is the fortuitous occurrence of a yellow-flowered species in *P. bathangensis*. The capsule in *P. Pauliana* is even more anomalous and recalls what is found in section Reinii; it far exceeds the calyx and is curved at the apex, in shape and consistency suggesting that of *Cerastium*. But length of capsule by itself is not an adequate criterion and other data in *P. Pauliana* do not support inclusion in Reinii. Finally the cytological observations of Bruun (*l.c.*) emphasise the special position of *P. Pauliana*, even to the extent of giving it subsectional rank, but do not advocate its exclusion from Cortusoides.

Seeds obtained by Forrest gave rise to flowering plants at Kew, Edinburgh, and elsewhere from 1923 onwards until at least 1932, but the species never became quite established and apparently it is now lost to cultivation.

A fairly robust sparsely hairy perennial. Leaves 3–9 to each plant, including the petiole 10–25 cm. long; lamina 3–10 cm. long and broad, in outline orbicular to broadly ovate, deeply cordate at the base, rather shallowly 7-lobed, the lobes acute very deeply dentate and ciliate, membranous in texture, dark green and glabrous above or with occasional septate hairs, pale green below with a few septate hairs along the nerves; midrib and 2–3 pairs of basal

or subbasal lateral nerves prominent on the lower surface; reticulation wide and poorly developed; petiole 7–18 cm. long, thinly covered with long articulated hairs. Scape 20–45 cm. tall, slender, well covered with pale tawny short septate hairs, carrying a lax raceme of 10–30 flowers; bracts 3–7 mm. long, sometimes adherent to the pedicel, lanceolate or sublinear or occasionally oblong, 3–4-lobulate towards the apex, with one prominent nerve, pubescent; pedicels 6–10 mm. long, hairy. Calyx 5–6 mm. long, campanulate, minutely puberulous, with five main prominent nerves, cut to the middle into triangular acuminate or apiculate lobes. Corolla pale yellow with the eye and tube orange, exannulate, heteromorphic; tube twice the length of calyx or even a little longer, narrowly cylindrical, ampliate above insertion of stamens; limb 1.5–2 cm. in diameter with obovate deeply emarginate lobes. Stamens, with anthers about 1 mm. long, inserted at the very apex of corolla-tube in thrum-eyed flowers, near base in pin-eyed. Long style equalling corolla-tube or slightly exserted; short style 1–2 mm. long. Capsule 1–1.5 cm. long, 2 or almost 3 times longer than calyx, oblong, curved at the apex and there dehiscing by longitudinal teeth, in texture parchment-like. Seeds 0.5 mm. in diameter, ovoid or rounded or even subquadrate, vesicular-surfaced.

Represented in the Edinburgh Herbarium by the type:—

S.W. SZECHWAN: Mountains S.E. of Yungning (*Forrest*, 22073—*type*, 22452).

P. septemloba Franch. in Bull. Soc. Bot. France, xxxii, 265 (1885); Pax in Engl. Bot. Jahrb., x, 169 (1889); Diels, *ibid.*, xxix, 520 (1900); Forbes and Hemsl. in Journ. Linn. Soc., xxvi, 42 (1889); Pax in Engl. Pflanzenr. Primulaceae, 30 (1905); Tribune Hort., ix, t. 411 (1914); Farrer, Engl. Rock Gard., ii, 181, 512 (1919); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 137, 144, fig. 46 (1913); *Forrest*, *ibid.*, xli, 203 (1915); Ward, *ibid.*, xlviii, 206–7 (1923); W. W. Sm. and *Forrest*, *ibid.*, liv, 17 (1929); Hand.-Mzt., *ibid.*, liv, 57 (1929); The Garden, lxxxvii, 209 (1923); Gard. Chron., lviii, 297, fig. 105 (1915); Ward, *ibid.*, lxxxviii, 8 (1930); W. W. Sm. and *Forrest* in Notes Roy. Bot. Gard. Edin., xvi, 20 (1928); Bruun, Cytological Studies in *Primula*, 24, 125 (1932); Hand.-Mzt. in Symb. Sin., vii, 734 (1936); Chen in Bull. Fan Mem. Inst. Biol., Bot. Ser., ix, 280 (1939).

The discovery of this species is due to Abbé Delavay who collected it in 1884 in woodland near the foot of the Lichiang glacier in

Yunnan. The type, *Delavay* 12, is in the Paris Herbarium. *P. septemloba* is now known to occur freely in N.W. Yunnan and S.W. Szechwan in moist shady situations in mixed forests at 3000–4300 m. In his diagnosis Franchet (*l.c.*) placed it in company with *P. geraniifolia*, *P. mollis*, and *P. Kaufmanniana*, noting that these four species are akin and are only discriminated by the characters of the foliage. In his Monograph Pax (*l.c.*, 21) likewise relies mainly on the leaf-characters in the construction of his key to the species of this alliance. Later Balfour (*l.c.*, 144) in formulating his section Geranioides associated *P. septemloba* with *P. geraniifolia* and *P. heucherifolia*. In these views and in those of subsequent commentators there is no divergence of any moment. Only in the cytological data (Bruun, *l.c.*) is there a suggestion that *P. septemloba* is more akin to *P. mollis* than to the two species just quoted. But in its general aspect it most resembles *P. geraniifolia* from which it differs in the monomorphic flowers. It was introduced to cultivation from seed collected by Forrest in 1906 and still persists.

A hairy perennial with a slender or sometimes stout horizontal rootstock. Leaves including the petiole 10–30 cm. long; lamina 5–15 cm. long and broad, orbicular in outline, very deeply cordate at the base, palmately 7–9-lobed, the lobes divided into lobules rounded at the apex and irregularly dentate, dark green above and thinly covered with septate hairs, paler green below with numerous outward spreading hairs along the veins; nerves slightly impressed above; midrib and 3 pairs of basal or subbasal lateral nerves conspicuous below; petiole 5–15 cm. long with dense tawny hairs. Scape 10–50 cm. long, slender or comparatively sturdy, thickening and lengthening at fruiting time, conspicuously hairy, carrying an umbel of 3–6 drooping flowers, or as many as 3 superposed umbels; bracts 5–10 mm. long, linear or lanceolate to narrowly oblong, pubescent; pedicels 5–20 mm. long, densely pubescent, more or less erect at fruiting time. Calyx 5–8 mm. long, campanulate to tubular-campanulate, usually purplish-tinted, glabrous or minutely puberulous, cut to about the middle into lanceolate apiculate teeth, each with one prominent nerve and often also with a pair of lateral nerves. Corolla deep purplish-rose to rose-crimson, annulate, monomorphic; tube twice the length of the calyx or even a little longer, cylindrical, ampliate above insertion of stamens; limb 6–12 mm. in diameter with suberect narrowly obcordate emarginate lobes. Stamens, with anthers 1 mm. long, inserted at apex of corolla-tube reaching annulus. Style as long as corolla-tube or slightly exserted beyond annulus. Capsule oblong, as long as or a

little longer than calyx, dehiscing by longitudinal valves. Seeds 1 mm. in diameter, ovoid to quadrate-angular, vesicular surfaced.

This species is represented in the Edinburgh Herbarium by the following collections:—

YUNNAN: Lichiang Range (*Forrest*, 2276, 5757, 10215, 30305); (Yü, 15265); Tali Range (*F.* 1811, 11615, 30192); (*McLaren's Native Collector*, 122); Bei ma Shan, Atuntze (Yü, 10843); Chungtien Plateau (*F.* 11161); Chienchuan-Mekong divide (*F.* 23252); Lanping Shan (*F.* 30295); slopes Mt. Gyi-na lo-ko (*Rock*, 25004); sine loc. (*F.* 6801, 28517).

SZECHWAN: Mountains between Litang and Yalung Rivers (*Rock*, 16672); Muti Kouka Snow Range, Muli (*R.* 23692, 24313).

var. **minor** Ward in *Ann. Bot.*, xlv, 123 (1930).

Differing chiefly from the type in having smaller more narrowly tubular flowers and in the monomorphism confined to the lower half of the corolla-tube.

Represented in the Edinburgh Herbarium by the co-type:—

ASSAM HIMALAYA: Mishmi Hills, Delei Valley (*Ward*, 8346—*co-type*).

P. vaginata Watt in *Journ. Linn. Soc.*, xx, 4 t. 2B (1882); Hook. f. in *Fl. Brit. Ind.*, iii, 484 (1882); Pax in *Engl. Bot. Jahrb.*, x, 169 (1889), and in *Engl. Pflanzenr. Primulaceae*, 32 (1905); Watt in *Journ. Roy. Hort. Soc.*, xxix, 301, 321 (1904), and in *ibid.*, xxxix, 202, 215-216 (1913); W. W. Sm. and Forrest, *ibid.*, liv, 17 (1929), and in *Notes Roy. Bot. Gard. Edin.*, xvi, 20 (1928); Ward in *Gard. Chron.*, lxxxviii, 9 (1930).

Primula vaginata was discovered seventy years ago by C. B. Clarke in the Sikkim Himalaya at Laghep where it grows at 3300 m. in woodland or on banks or in the shade of rocks. It appears to be limited to Eastern Sikkim, with one record from the adjoining Tibetan valley of Chumbi. When a description of it was published in 1882 neither Watt nor Hooker quoted any near ally, but Hooker (*l.c.*, 483) mentioned it along with four other species as in the company of *P. sinensis*. An adequate figure is furnished by Watt, based on the type, *Clarke* 27774, in Kew Herbarium. The plant is one of a trio of species well distinguished by the conspicuous inflation of the base of the petiole. This feature is utilised by Pax (*l.c.*, 32) in the key to the species of his section *Sinenses*. The kinship of *P. vaginata* with *P. eucyclia* and *P. Normaniana* does not depend on this single criterion but is clearly evidenced by the similarity in foliage and in flowers. The nearer ally is *P. eucyclia* which is somewhat slenderer, carries as a rule two flowers only on the scape

and these larger than in *P. vaginata*. *P. Normaniana* is more vigorous than either of the above with a very compact inflorescence almost simulating a capitulum. Seed of *P. vaginata* has been obtained once or twice, but no success in culture has been achieved. In its own area it can be confused in autumn with *P. geraniifolia*; seeds presumed to come from *P. vaginata* have on several occasions given rise at Edinburgh to the commoner species.

A small more or less pubescent or finely scabrid perennial with a long thin creeping rhizome. Leaves including the petiole 2–10 cm. long at flowering time, up to 20 cm. long at fruiting time; lamina 1–5 cm. long and broad, orbicular, deeply cordate at the base, palmately 7-lobed, the lobes deeply dentate, often tridentate, with the teeth acute or obtuse, the sinuses between the lobes often with a conspicuous tooth, dark green and pubescent sometimes scabrous above, light green and glabrous below; midrib and 3 pairs of basal or subbasal lateral nerves conspicuous below; reticulation obscure; petiole 1–10 cm. long, glabrous or faintly pubescent, abruptly dilated into a sheath, membranous and 5 mm. broad. Scape 6–12 cm. long, puberulous, slender, thicker and a little longer at fruiting time, carrying a head of 2–9 flowers; bracts 3–6 mm. long, linear to linear-lanceolate, at first puberulous and ciliolate, later glabrous; pedicels 5–10 mm. long, pubescent, erect or suberect, slender, thickening and slightly elongating at fruiting stage. Calyx 3–5 mm. long, campanulate, finely pilose but ultimately glabrous, cut to the middle into ovate to ovate-lanceolate acute or obtuse often recurved lobes, each with one conspicuous nerve and markedly ciliate at the margin. Corolla lilac to rosy purple, annulate, heteromorphic; tube slightly longer than calyx or nearly twice as long, cylindrical, ampliate above insertion of stamens; limb about 1 cm. in diameter with bilobulate lobes, the lobules usually bidentate. Stamens, with anthers a little over 1 mm. long, inserted at apex of corolla-tube and slightly exerted beyond annulus in thrum-eyed flowers, at middle of tube in pin-eyed. Long style reaching annulus; short style half the length of corolla-tube. Capsule globose, hardly as long as calyx, dehiscing rather irregularly by longitudinal valves. Seeds 0.75 mm. in diameter, quadrate-angular or angularly ovoid, vesicular-surfaced.

The species is represented in the Edinburgh Herbarium by the following collections:—

SIKKIM: Laghep (*W. W. Smith*, 3292; *Cooper*, 562); Karponang (*Cooper*, 5); Kanglasa (*Cave*, 2356, 2362).

S. TIBET: Chumbi Valley (*Cooper*, 777).

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THE GENUS PRIMULA: SECTION MALVACEA Balf. fl.
By W. WRIGHT SMITH and H. R. FLETCHER.

(Read 18th May 1944.)

In 1913 at the Third Primula Conference Balfour (1) in his tentative analysis of the Chinese species made *P. malvacea* the centre of a small section in which he included five other names—*P. bathangensis*, *P. blattariformis*, *P. neurocalyx*, *P. pinchouanensis*, and *P. racemosa*. But he was not prepared to vouch for the validity of all these as distinct species. Three of the names are given by Pax (2) in his Monograph as members of the section Sinenses, and within the very wide field of that section they were not inaptly placed. The propriety of dividing the Paxian section Sinenses into smaller sections is discussed in some detail under section Cortusoides and need not be repeated here. Under the same section will be found a general statement of the characters which are common to the kindred small sections, Sinenses, Obconica, Malvacea, Pycnoloba, and Reinii, with a summary of the variations in calycine structure which serve to separate them.

The first outline of the section Malvacea by Balfour (1) was not accompanied by any definition, but was based mainly on the content already quoted. He took, however, an early opportunity of supplementing the original statement and in his description of *P. celsiaeformis* (3) there is appended: "The Malvacea series of Primula is a compact and definite one. The species are all herbaceous forms with coarse leaves and long racemose inflorescences bearing flowers the calyx of which is diagnostic. It is foliaceous with well-developed reticulate venation more or less elevated, and the obconical tube expands into broad spreading lobes. In fruit the whole enlarges to form a platter-like expansion in the middle of which rests the globose capsule, the wall of which is thickened throughout its whole extent." He took occasion at the same time to revise the content, although lack of material precluded any assured conclusions. He was able, however, to equate *P. racemosa* with *P. bathangensis* and advocated the removal of *P. neurocalyx* from the section to proximity with *P. mollis*. (The correct position of *P. neurocalyx* is yet to be solved, but the problem is discussed under *P. malvacea*, q.v.)

At the Fourth Primula Conference in 1928 the content of the

section was given another re-arrangement by Smith and Forrest (4), but the species included did not receive detailed analysis. *P. neurocalyx* was retained by them within the section, but no further evidence was available for its elucidation. Their addition of *P. aromatica* to the section is no longer upheld, for that somewhat anomalous species is better associated with Malacoides.

Acquaintance with the species in culture has tended to approve the sectional status of Malvacea, and Stapf (5) in his comments on *P. blattariformis* and *P. bathangensis* has expressed the view that "these two species are characteristic representatives of a very natural group of Primulas, confined to south-western China and distinguished by their general habit as well as by the peculiar development of the maturing calyx, whose limb—that is the part situated above the ovary—becomes much enlarged often into a platter-like shape and prominently net-nerved, retaining, however, its herbaceous texture. They are all apparently plants of arid situations between altitudes of 6000–10,000 feet (rarely higher), and the failure to establish them in gardens may be connected with this circumstance."

The affinities of Malvacea are obviously with the sections mentioned above, and of these possibly *Obconica* comes nearest. The cytological data for Malvacea are not as yet investigated.

In the previous review of Smith and Forrest (4) some seven synonyms are dealt with, and in the present statement the process of reduction has been carried further. (Arguments in support will be found under the general account of *P. malvacea* and also in that of *P. cinerascens* in section *Cortusoides* where *P. riparia* is considered.) The net result is a section of only five species.

REFERENCES.

- (1) BALFOUR in Journ. Roy. Hort. Soc., xxxix, 145 (1913).
- (2) PAX in Engl. Pflanzenr. Primulaceae, 20, 26 (1905).
- (3) BALFOUR in Notes Roy. Bot. Gard. Edin., ix, 9 (1915).
- (4) SMITH and FORREST, *ibid.*, xvi, 27 (1928), and in Journ. Roy. Hort. Soc., liv, 18 (1929).
- (5) STAPF in Bot. Mag., 8893 (1938).

KEY TO THE SPECIES.

A. Flowers rose-purple, lilac or white:

B. Lamina suborbicular, as broad as long; petiole longer than lamina;
inflorescence usually verticillate *malvacea*

BB. Lamina obovate to elliptic, longer than broad; inflorescence usually
racemose:

C. Lamina tapering to rounded at base, much longer than petiole;
reticulation not prominent below *blattariformis*

- CC. Lamina cordate at base, much shorter than petiole; reticulation markedly elevate below *celsiaeformis*
- AA. Flowers yellow, nearly always in racemes:
- B. Lamina reniform, as broad as long; petiole longer than lamina. *bathangensis*
- BB. Lamina obovate to elliptic, longer than broad; petiole shorter than lamina *saturata*

P. bathangensis Petitm. in Bull. Herb. Boiss., Ser. ii, viii, 365 (1908); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 131, 145, 146 (1913), and in Notes Roy. Bot. Gard. Edin., ix, 9 (1915); Hand.-Mzt. in Medd. Göt. Bot. Trad., ii, 103 (1926); W. W. Sm. and Forrest in Journ. Roy. Hort. Soc., liv, 19, fig. 10 (1929); Hand.-Mzt., *ibid.*, liv, 53 (1929); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 27 (1928); Hand.-Mzt. in Symb. Sin., vii, 736 (1936); Hall in Gard. Chron., ciii, 254 (1938); Stapf and Ballard in Bot. Mag., t. 8895 (1938); Chen in Bull. Fan Inst. Biol., Bot. Ser., ix, No. 5, 288 (1939); Fletcher in Gardening Illust., lxiii, 492, with fig. (1941); *P. pintchouanensis* Petitm. in Bull. Herb. Boiss., viii, 364 (1908); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 136, 145, 146 (1913); W. W. Sm. and Forrest, *ibid.*, liv, 20 (1929); Balf. f. in Notes Roy. Bot. Gard. Edin., ix, 9 (1915); W. W. Sm. and Forrest, *ibid.*, xvi, 27 (1928). *P. racemosa* Bonati in Bull. Soc. Bot. Fr., ix, 484 (1909); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 136, 145, 146 (1913), and in Notes Roy. Bot. Gard. Edin., ix, 9 (1915); W. W. Sm. and Forrest, *ibid.*, xvi, 27 (1928), and in Journ. Roy. Hort. Soc., liv, 20 (1929). *P. stephanocalyx* Hand.-Mzt. in Anz. Akad. Wiss. Wien, Math.-Nat., lx, 136 (1923), and *ibid.*, lxi, 85 (1924), and in Symb. Sin., vii, 736 (1936); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 27 (1928), and in Journ. Roy. Hort. Soc., liv, 20 (1929).

As noted by Stapf (Bot. Mag., *l.c.*), "this striking *Primula* became known simultaneously (1908) from two very distant localities and under two distinct names, bestowed on it by the same author, M. Petitmengin, namely *P. pintchouanensis*, collected by Jean Py in the neighbourhood of Pinchwanchow, about twenty miles east of the Lake of Tali in Yunnan, and *P. bathangensis*, collected by the Abbé Soulié at Batang (or Bathang) in Western Szechwan, near the Tibetan frontier." With the two names having equal validity, the choice appears to have fallen on *P. bathangensis*. The type, *Soulié* 3769, is in the Paris Herbarium. Petitmengin associated his plant with *P. malvacea* and *P. blattariformis*, distinguishing it among other characters by the yellow flowers. A certain dubiety existed for some years as to whether Petitmengin's two names represented a

single species (Balfour, *l.c.*), but the area of distribution is now known to be continuous and the alternative name is generally accepted as a synonym. Two further names are unquestionably synonymous—*P. racemosa* and *P. stephanocalyx*. As regards the two allies quoted above and apart from the flower-colour, it may be said that *P. bathangensis* has the leaf-shape and long petioles of *P. malvacea* but the inflorescence of *P. blattariformis*. What may be reckoned an even closer ally is the yellow-flowered *P. saturata*, described in this review; it in its turn may be said to have the leaf shape, short petioles, and racemose inflorescence of *P. blattariformis*, and therefore deviates from *P. bathangensis* in leaf shape and in the short petioles as well as in the deeper orange of the corolla. In these allied species there is certainly the suggestion of a Mendelian distribution of characters at some time in the past.

The first introduction of this species to cultivation is due to Forrest who sent ample seed home on at least six occasions between 1913 and 1922. The resultant plants persisted for a few years, but were reluctant to seed in culture though amenable to propagation by root cuttings. Further seed was obtained from West China in 1934 and plants therefrom are not wholly lost.

A robust perennial with a short comparatively stout rhizome and a spreading tuft of 3–5 leaves. Leaves including the petiole 7–30 cm. long; lamina 3–12 cm. long, up to 18 cm. at fruiting time, 2–14 cm. broad, up to 24 cm. in fruit, reniform, very deeply cordate at the base, repand-crenate or lobulate and denticulate at the margin, bullate and sparingly scabrid-pubescent above, densely and shortly pilose below especially along the veins; nerves impressed above; midrib and 3–4 pairs of lateral nerves (2 pairs basal) conspicuous below; petiole 3–25 cm. long, stout and hard, markedly pilose. Scape 10–70 cm. tall, sturdy and erect, 1–4 to each plant, conspicuously pilose, floriferous for over half its length, carrying usually numerous flowers arranged in a long rather lax raceme, or sometimes in semi-whorls; bracts 5–15 mm. long, pilose, the upper lanceolate to linear, the lower ovate to elliptical and foliaceous; pedicels 5–15 mm. long, pilose, in fruit thickening and lengthening up to 30 mm. Calyx 7–10 mm. deep (in fruit nearly 2 cm. deep), 1–1.5 cm. wide at the apex, foliaceous, very widely campanulate, sometimes patent or even reflexed, conspicuously pilose, often very elegantly veined, enlarging up to 3 cm. wide at fruiting time, cut to a third or to a half into ovate or triangular entire or denticulate acute lobes. Corolla yellow to golden-orange, annulate, heteromorphic; tube 1–2 times the length of the calyx, cylindrical, amplate above

insertion of stamens; limb 1.5 to nearly 3 cm. in diameter with obcordate deeply emarginate lobes. Stamens, with anthers 1.5 mm. long, inserted at middle of tube, or slightly lower in pin-eyed flowers; near the apex, but not reaching annulus in thrum-eyed. Long style as long as corolla-tube or a little shorter; short style half as long as tube or only 1 mm. long. Capsule 5-7 mm. in diameter, subglobose or shortly oblong, dehiscent by 5 acute erect teeth. Seeds scarcely exceeding 0.5 mm. in diameter, ovoid to quadrate-angular, reticulate-surfaced or vesicular-surfaced.

This species is represented in the Edinburgh Herbarium by the following collections:—

YUNNAN: Mountains N.E. of the Yangtze bend (*Forrest*, 10720, 12660, 15247); Lichiang Range (*F.* 28216); Yangtze valley, north of Feng-kou (*F.* 20665); Bey-ti Shan (*F.* 20523); mountains north of Yung-peh (*F.* 23165); Yun-lu Shan, S.W. of Lichiang, Yangtze-Mekong watershed (*Rock*, 25070); Schou-tschu, Yangtze (*Hand.-Mzt.*, 7593—*co-type* of *P. stephanocalyx*); Yungning (*McLaren*, 200); sine loc. (*Ducloux*, 6949); (*Siméon Ten*, 294).

SZECHWAN: Mountains around Muli (*Forrest*, 16479, 22168); Hokeo, Tatsienlu district (*Cunningham*, 570).

P. blattariformis Franch. in *Gard. Chron.*, i, 575 (1887); Franch. in *Bull. Soc. Bot. Fr.*, xxxv, 430 (1888); Forbes and Hemsl. in *Journ. Linn. Soc.*, xxvi, 37 (1889); Pax in *Engl. Bot. Jahrb.*, x, 167 (1889), and in *Engl. Pflanzenr. Primulaceae*, 26 (1905); Balf. f. in *Journ. Roy. Hort. Soc.*, xxxix, 132, 145 (1913); *Forrest*, *ibid.*, xli, 205 (1915), and in *Gard. Chron.*, lix, 254, fig. 106 (1916); Balf. f. in *Notes Roy. Bot. Gard. Edin.*, ix, 8 (1915); Kingdon Ward in *Journ. Roy. Hort. Soc.*, xlviii, 206 (1925); W. W. Sm. and *Forrest*, *ibid.*, liv, 19 (1929), and in *Notes Roy. Bot. Gard. Edin.*, xvi, 27 (1928); *Hand.-Mzt.* in *Journ. Roy. Hort. Soc.*, liv, 55 (1929), and in *Symb. Sin.*, vii, 736 (1936); Stapf and Ballard in *Bot. Mag.*, t. 8893 (1938); Wilkie in *Gard. Chron.*, cx, 73, fig. 38 (1941); Fletcher in *Gardening Illust.*, lxiii, 492, with fig. (1941). *P. microstachys* Balf. f. et *Forrest* in *Notes Roy. Bot. Gard. Edin.*, xiv, 49 (1923); W. W. Sm. and *Forrest*, *ibid.*, xvi, 27 (1928), and in *Journ. Roy. Hort. Soc.*, liv, 20 (1929).

This species, like *P. malvacea*, was one of the discoveries of the Abbé Delavay who collected it in 1885 on the limestone pastures of Che-tcho-tze, near Tapintze, to the north-east of Tali. The type, *Delavay* 2092, is in the Paris Herbarium. The distribution of this

Primula is confined to N.W. Yunnan and to an area around Muli in S.W. Szechwan. It occurs at altitudes of 2000-3700 m., sometimes in company with *P. malvacea*, its nearest ally, from which it differs in the form of the leaves, in the short petioles, and in the elongate racemose inflorescence. According to Forrest (*l.c.*, 254) the plant is "a lover of dry shade, nestling in the most secluded situations of arid rock gutters on the mountain sides, closed in more or less by sheltering scrub, or under the shade of heavy boulders on the banks of mountain torrents." Seed was obtained by Forrest in 1913-14 and the resultant plants continued for some years. The species is not long-lived, is shy to set seed and difficult to keep even in the shelter of a cool greenhouse. It is still in cultivation at Edinburgh from seed received a few years ago from West China. The main features of the species are well shown in the Botanical Magazine figure (*l.c.*). *P. microstachys* must be regarded as synonymous. It is of dwarf habit with very slender flowers, but differs in no character except in the size of its parts.

A hairy perennial with a basal rosette of leaves and a short comparatively stout rhizome. Leaves including the petiole 3-20 cm. long; lamina 2.5-14 cm. long, 1.5-10 cm. broad, elliptic-oblong to obovate, rounded at the apex, rounded or slightly tapering or occasionally subcordate at the base, irregularly crenate or undulate or shallowly lobed with the lobes denticulate, dark green, pubescent and more or less bullate on the upper surface, paler below and markedly hirsute especially along the veins; midrib and 6-8 pairs of lateral nerves prominent below; petiole 0.5-6 cm. long, very hirsute, membranously winged, more or less sheathing at the base. Scape 10-55 cm. long, sturdy and erect, thickening at late flowering and fruiting stage, carrying a more or less secund raceme of numerous fragrant flowers; bracts 5-10 mm. long, lanceolate, hirsute, at fruiting time sometimes enlarging up to 1.5 cm. long and 5 mm. broad, and then ovate to elliptic and denticulate; pedicels quite short at first but increasing up to 15 mm., hirsute. Calyx 5-15 mm. deep, 5-20 mm. wide at the apex, widely campanulate, softly scabrid, prominently veined, cut to the middle or almost so into triangular to broadly ovate spreading lobes, more or less obtuse at the apex but mucronate, ciliate and often denticulate at the margin, enlarging at fruiting time and then as much as 2.5 cm. in diameter. Corolla pale or dark lavender-rose to purplish-pink with a yellow or greenish eye, annulate, heteromorphic; tube sometimes no longer than the calyx but more usually about twice as long, cylindrical, ampliate above insertion of stamens, pubescent without;

limb 1.5–2.5 cm. in diameter with obcordate emarginate lobes. Stamens, with anthers 1.5 mm. long, inserted near apex of corolla-tube, barely reaching the annulus, in thrum-eyed flowers, near middle of tube in pin-eyed. Long style a little shorter than corolla-tube; short style about half the length of the tube or a little shorter. Capsule 5–7 mm. diameter, subglobose, well enclosed in base of calyx-tube, dehiscing by 5 or 10 longitudinal valves. Seeds as in *P. malvacea*, 1 mm. long, reticulate-surfaced.

This species is represented in the Edinburgh Herbarium by the following collections:—

YUNNAN: Langkong mountains, above Tapintze (*Delavay*, 2092—*co-type*); Langkong Gorge (*Forrest*, 9985); descent of the Yangtze from the eastern boundary of the Lichiang Valley (*F.* 10794); Ghi-Shan, east of Tali Lake (*F.* 13491); Western flank of the Tali Range (*F.* 11594); Mountains north of Yung-peh (*F.* 23123, 23167); Chienchuan-Mekong divide (*F.* 23056); Mekong-Yangtze divide (*F.* 13137—*type* of *P. microstachys*); East Mt. of Chêngh nan (*McLaren's Collector*, 57A); sine loc. (*Forrest*, 30665).

S.W. SZECHWAN: Muli Mountains (*Forrest*, 16497, 16830); Muli (*Ward*, 4520); Muli, near Lama-sery (*Yü*, 14854); near Muli (*Hand.-Mzt.*, 7263); Mountains west of Muli (*F.* 22139); Mount Mitzuga, Muli (*Rock*, 16257, 23981, 24543).

P. blattariformis subsp. ***Tenana*** (Bonati ex Balf. f.) W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 27 (1928), and in Journ. Roy. Hort. Soc., liv, 20 (1929). *P. Tenana* Bonati ex Balf. f. in Notes Roy. Bot. Gard. Edin., ix, 9 (1915). *P. blattariformis* var. *Duclouxii* Bonati in Bull. Soc. Bot. France, ix, 465 (1909); Balf. f. in Notes Roy. Bot. Gard. Edin., ix, 9 (1915).

There are difficulties in the assessment of this plant. It may be no more than a dwarf state of *P. blattariformis*. The locality is uncertain or at any rate has not been identified by us as a place name. The collector, Siméon Ten, usually worked in Eastern Yunnan and it is quite likely that the plant came from outwith the recorded area for *P. blattariformis*. The type is in the Paris Herbarium under *Ducloux* 556 and was at first named *P. blattariformis* var. *Duclouxii* by Bonati. This we have not seen but only a photograph of what is presumably a co-type and annotated by Bonati. According to the latter (*l.c.*) and to Balfour (*l.c.*) the plant differs from *P. blattariformis* in the soft non-scabrid leaves, 4–5 cm. long, 3–4 cm. broad, cordate at the base, deeply lobate, with rounded lobes; in the scabrid scape which is not lanate; in the

longer pedicels, 1-2 cm.; in the broader bracts much shorter than the calyx; in the smaller flowers and in the shape of the calyx measuring 1-2 cm. in diameter after flowering. But these criteria are not very convincing and the photograph suggests that it is no more divergent than *P. microstachys* from the typical plant. A scrutiny of the original material will probably confirm that view.

Represented in the Edinburgh Herbarium by a photograph of a *co-type*:—

YUNNAN: Makong near Tong-Tchouan (*Siméon Ten*).

P. celsiaeformis Balf. f. in Notes Roy. Bot. Gard. Edin., ix, 7 (1915); W. W. Sm. and Forrest, *ibid.*, xvi, 27 (1928), and in Journ. Roy. Hort. Soc., liv, 20 (1929); Hand.-Mzt. in Symb. Sin., vii, 736 (1936). *P. racemosa* Lévl. in Le Monde des Plantes, xvii, No. 92, 2 (1915)—non Bonati.

The material on which this species is based was collected by E. E. Maire about 1913 on rocky ground in Eastern Yunnan at the low elevation of 600 m. Some of the specimens were sent to Lévillé and some to Edinburgh, with the result that two descriptions appeared in 1915. The name chosen by Lévillé and the first to be published, *P. racemosa*, is preoccupied, for Bonati used the specific term in 1909. *P. celsiaeformis* finds its nearest ally in *P. blattariiformis*, from which it differs in the long petioles and in the cordate base of the lamina which is markedly favose-reticulate below and also very glandular. It has been obtained only on the one occasion and in an area somewhat remote from that of its ally, which grows moreover at much higher elevations. On the evidence available it certainly does not merge into *P. blattariiformis*, but a wider range of specimens from Eastern Yunnan is desirable. It has not been in cultivation.

A robust glandular hairy perennial with a short stout rhizome. Leaves including the petiole 10-24 cm. long; lamina 4-10 cm. long, 2-5 cm. broad, oblong to oblong-elliptic, rounded or obtuse at the apex, cordate or subcordate at the base, undulate-crenate at the margin with the crenations denticulate, bullate above and sprinkled with short white scabrid hairs, covered below with short tawny hairs especially along the main nerves and with numerous round minutely stipitate amber glands; midrib, 7-10 pairs of lateral nerves and reticulation impressed above, conspicuous and sometimes elevated below; petiole 4-15 cm. long, pubescent, tomentose or even lanate, vaginate at the base. Scape 30-45 cm. tall, sturdy, glandular, hirsute-tomentose, carrying a long raceme of numerous flowers; bracts 4-6 mm. long, up to 12 mm. long at fruiting time,

linear-subulate or lanceolate to oblanceolate, glandular-hairy; pedicels 7–15 mm. long, up to 20 mm. in fruit, horizontal or suberect, glandular-hairy. Calyx 7–8 mm. long, 7–10 mm. wide at the apex, broadly campanulate, conspicuously scabrid-hairy within and without, prominently veined, cut to the middle into broadly triangular to ovate spreading lobes acute or obtuse at the apex, markedly accrescent and at fruiting time up to nearly 2 cm. long, and 2.5 cm. across at the apex, strongly reflexed, bullate on the inner surface, elegantly reticulate-veined on the outer. Corolla violet, annulate, heteromorphic; tube 2 to nearly 3 times the length of the calyx, cylindrical, very slightly ampliate above insertion of stamens; limb 1.5–2.5 cm. in diameter with obcordate emarginate lobes. Stamens, with anthers 1.5 mm. long, inserted slightly below middle of corolla-tube in pin-eyed flowers. Long style about two-thirds the length of corolla-tube. Capsule more or less globose, 4–5 mm. in diameter, dehiscing by 5 longitudinal valves. Seeds about 0.75 mm. in diameter, ovoid or quadrate-angled, obscurely reticulate-surfaced.

This species is represented in the Edinburgh Herbarium by the following:—

N.E. YUNNAN: Rocks of Ta-tchai (*Maire*—*type* and *type* of *P. racemosa*).

P. malvacea Franch. in Bull. Soc. Bot. Fr., xxxiii, 65 (1886); Forbes and Hemsl. in Journ. Linn. Soc., xxvi, 39 (1889); Pax in Engl. Bot. Jahrb., x, 167 (1889), and in Engl. Pflanzenr. Primulaceae, 26 (1905); Tribune Hort., ix, 411 (1914); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 134, 145–6, fig. 49 (1913); Forrest, *ibid.*, xli, 205 (1915); W. W. Sm. and Forrest, *ibid.*, liv, 19, fig. 9 (1929), and in Notes Roy. Bot. Gard. Edin., xvi, 27 (1928); Farrer, Engl. Rock Gard., ii, 168 (1919); Hand.-Mzt., Symb. Sin., vii, 736 (1936). *P. neurocalyx* Franch. in Journ. de Bot., ix, 449 (1895); Pax in Engl. Pflanzenr. Primulaceae, 26 (1905); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 135, 145–6 (1913), and in Notes Roy. Bot. Gard. Edin., ix, 9 (1915); Farrer, Engl. Rock Gard., ii, 159 (1919); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 27 (1928), and in Journ. Roy. Hort. Soc., liv, 12, 20 (1929). *P. Rosthornii* Diels in Engl. Bot. Jahrb., xxix, 520 (1900); Pax in Engl. Pflanzenr. Primulaceae, 24 (1905); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 137, 145 (1913). *P. malvacea* subsp. *Rosthornii* (Diels) W. W. Sm. and Forrest in Journ. Roy.

Hort. Soc., liv, 19 (1929), and in Notes Roy. Bot. Gard. Edin., xvi, 27 (1928). *P. langkongensis* Forrest in Notes Roy. Bot. Gard. Edin., iv, 216, pl. xxvi (1908); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 134 (1913). *P. malvacea* var. *intermedia* W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xiv, 48 (1923), and *ibid.*, lvi, 27 (1928), and in Journ. Roy. Hort. Soc., liv, 19 (1929). *P. barybotrys* Hand.-Mzt. in Anz. Akad. Wiss. Wien, lx, 116 (1923), in Journ. Roy. Hort. Soc., liv, 53 (1929), and in Symb. Sin., vii, 736 (1936); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 27 (1928), and in Journ. Roy. Hort. Soc., liv, 19 (1929). *P. atrotubata* W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xiv, 33 (1923); W. W. Sm. and Forrest, *ibid.*, xvi, 27 (1928), and in Journ. Roy. Hort. Soc., liv, 19 (1929).

The first collection of this species was made by Delavay in 1883 on calcareous alpine rocks at Hee-gni-chao near Hoking in Western Yunnan. The type, *Delavay* 82, is in the Paris Herbarium. In his diagnosis Franchet comments on the peculiar character of the calyx which at maturity is dilated into a wheel-like form, comparable in his view to the calyx of *Androsace maxima*. He places the species near *P. mollis* in its general habit. The measurements given by him are much in excess of anything in the cotype at Edinburgh or in the specimens secured by Delavay in 1885 at Tapintze, but they are quite in accord with those available in the Lichiang material of Forrest. Franchet took his data from the larger plants, and the species is now known to show a high degree of variation in size according to environment and altitude. Pax (*l.c.*, 26) adds nothing of moment except an obvious correction of the size of the corolla as given by Franchet. Balfour (*l.c.*) proposes *P. malvacea* as the type of a section of that name and points out that the plant was brought into cultivation in 1908 by Forrest who described and figured it in the same year as *P. langkongensis* (*q.v.*). The classic locality for the species was visited on several occasions by Forrest and by Rock, and these explorers found in addition to normal specimens some with a very large toothed calyx and some with white flowers. The latter came into culture in 1933 at Edinburgh and have flowered yearly since. Another variation is shown in the large collections now available and that is the transition from a succession of whorls in the inflorescence to a racemose arrangement. In most plants the flowers are in whorls; in some they are almost but not quite in racemes; in others there is a mixture, as is exemplified by the figure given by Smith and Forrest (*l.c.*, fig. 9).

Here it will be expedient to deal in sequence with the synonyms quoted above and to consider how far these reductions are justifiable. The first of these is *P. neurocalyx* and that Franchetian plant presents a difficult problem. It was collected by Farges at Tchen-kéou-tin (Chengkow) in N. Szechwan about the same time and about the same place as *P. cinerascens* and they were described in the same publication without any suggestion of relationship between them. There is, however, evidence that the Farges material of the two plants was somehow intermixed, and there is no doubt that in their vegetative features the two show a marked resemblance. Franchet does not quote any numbered sheet of Farges in his diagnosis, but in the Paris Herbarium there is *Farges* 1365, written up by Franchet himself as *P. neurocalyx*. This was on loan to Balfour (about 1915) as the type and a photograph taken. The details as shown in this photograph are quite in conformity with Franchet's description and give the impression of a dwarf *P. malvacea* or almost exactly a *P. Rosthornii*. Franchet makes comparison only with *P. pycnoloba*. It seems strange that he omits any reference to *P. malvacea* described by him nine years before from Yunnan! Subsequently (about 1908) duplicates were presented to Kew and to Edinburgh under *P. neurocalyx*, written up (apparently) by Gagnepain and certified in one instance by Petitmengin. After repeated careful scrutinies of this material one can only conclude that it does *not* represent *Farges* 1365 but is almost certainly a state of *P. cinerascens*. (See also that species and *P. riparia* in section *Cortusoides*.) Pax (*l.c.*, 26) being without material relies on Franchet's diagnosis and concludes that the affinity lies with *P. pycnoloba*, *P. Rosthornii*, and *P. cinerascens*. In 1913 Balfour (*l.c.*, 145) places *P. neurocalyx* in his section *Malvacea* and accepts *P. Rosthornii* as a synonym of it, but only on the authority of Petitmengin. Any statement by Petitmengin on this point we have failed to trace. But the specimens of "presumed" *P. neurocalyx* continued their influence, for in 1915 Balfour (*l.c.*, 9) suggested relegation of the species to kinship with *P. mollis* and referred his species *P. riparia* to close proximity with it, while Smith and Forrest's treatment (*l.c.*, 27) retained it within *Malvacea*. So far then, on the evidence, we have to view *P. neurocalyx* as facing *P. malvacea* on one side and *P. cinerascens* on the other.

The next name to come into the problem is *P. Rosthornii*, described in 1900 and placed near *P. cinerascens* and *P. mollis*. The type is in the Berlin Herbarium and was collected in Eastern

Szechwan at Nanchwan, some 200 miles to the south of Chengkow. It was on loan to Edinburgh in 1928, and was found by Smith and Forrest (*l.c.*, 27) to be identical with what these two authors had described in 1923 as *P. malvacea* var. *intermedia*; it appears in their list as a subspecies of *P. malvacea*. This is the first indication that there is a close link between the slender plants under *P. neurocalyx* and *P. Rosthornii* from N. and E. Szechwan with the usually more robust plants of *P. malvacea* from Yunnan and S.W. Szechwan, and there is a strong presumption that only one broad species is in question. But only a revision, at present impossible, of the Farges material in Paris would be conclusive.

P. langkongensis as a synonym requires little comment, for Forrest realised soon after publication that his plant was none other than *P. malvacea* and that it came from near Delavay's original locality. The white variety known as *P. malvacea* var. *alba* occurs in the type country as well as in S.W. Szechwan and can be either robust or slender. *P. malvacea* var. *intermedia* is equivalent to *P. Rosthornii*, is found on stony pastures and on limestone cliffs in the Muli district of S.W. Szechwan and also in Yunnan, and in such environments can be dwarfer than anything so far collected under *P. neurocalyx* or *P. Rosthornii*.

In 1923 appeared two further specific names—both based on plants collected in S.W. Szechwan near or not far from Muli. *P. barybotrys* is described as akin to *P. celsiaeformis*, *P. Tenana*, *P. malvacea*, and *P. blattariformis*, but differs from all except *P. malvacea* in the shape of the leaves. The type, *Handel-Mazzetti* 7382, is in the Vienna Herbarium. This we have seen and retain a photograph of it. At first inspection it appears to deviate markedly from *P. malvacea* in the inflorescence which is more racemose than whorled. But this tendency to racemose development is manifest also in *P. malvacea*, both in the wild and in culture. It can be seen even in *Delavay* 82, the original collection! The other specific name, *P. atrotubata*, described by Smith and Forrest (*l.c.*) was reduced by them in 1928 (*l.c.*) to *P. barybotrys*, following exchange of views with Handel-Mazzetti. This Muli plant cannot be separated from the typical *P. malvacea* as it occurs in N.W. Yunnan, except on the very slender criterion that its inflorescence is more often racemose than whorled, while in the other it is more whorled than racemose!

The reductions advocated above may appear to be drastic, but with the abundant specimens now before us such a course seems entirely justified. Some dubiety may persist as to the exact

significance of *P. neurocalyx*, while the Muli plant under *P. barybotrys* may yet be accorded a measure of varietal status.

The species is confined to Yunnan and Szechwan at altitudes of 2300–3700 m. Its foliage characters separate it from *P. blattariiformis*, while *P. bathangensis* differs in its racemose inflorescence of yellow flowers. It was brought into culture in 1908 in its typical form but did not persist for long. A white variety has held its own for the last ten years but is rare.

A robust but often quite dwarf more or less hairy perennial with a short stout rhizome. Leaves including the petiole 3–30 cm. long; lamina 1.5–12 cm. long and broad, very broadly ovate to sub-orbicular, rounded at the apex, deeply cordate at the base, undulate-crenate or deeply crenate-lobulate at the margin, the lobules minutely denticulate or subcrenulate, bullate and sparsely or copiously pubescent above, hirsute below especially along the veins and thinly covered with sessile amber glands; nerves impressed above; midrib and 4–5 pairs of lateral nerves prominent below; petiole 1–22 cm. long, usually copiously covered with long white or tawny septate hairs, vaginate at the very base. Scape 3–40 cm. high, sometimes slender, more usually sturdy and erect, thickening at fruiting time, markedly pilose, carrying an elongate inflorescence with the flowers arranged commonly in 1–8 verticels, but sometimes in pseudo-verticels or even in a raceme; bracts 5–20 mm. long, 2–10 mm. broad, subfoliaceous, lanceolate or oblanceolate or broadly ovate, acute or obtuse or apiculate at the apex, entire or toothed, hairy; pedicels 5–35 mm. long, horizontal or semi-erect, very pilose. Calyx 8–15 mm. long and broad, accrescent in fruit and then up to 20 mm. long and 35 mm. across the apex, very widely campanulate, very hairy on both surfaces, covered with sessile amber glands without, cut to the middle or well below into broadly ovate to oblong lobes, rounded or obtuse or acute at the apex, entire or obviously toothed at the margin, prominently veined, markedly patent at the fruiting stage. Corolla pale or dark rose, occasionally blue with a yellow or greenish-yellow eye, annulate, heteromorphic; tube usually subequal to the calyx, occasionally quite obviously longer or shorter than the calyx, somewhat hairy without, broadly cylindrical, ampliate above insertion of stamens; limb 1.5–2.5 cm. in diameter with obcordate emarginate lobes. Stamens, with anthers 1.5 mm. long, inserted in lower half of corolla-tube in pin-eyed flowers, in upper half in thrum-eyed. Long style about two-thirds the length of corolla-tube; short style one-third the length of tube. Capsule 4–6 mm. in

diameter, globose, more or less enclosed in tubular base of calyx, dehiscing by longitudinal valves. Seeds about 1 mm. in diameter, somewhat flattened, ovoid to cuboid, reticulate-surfaced.

P. malvacea is well represented in the Edinburgh Herbarium by the following collections:—

YUNNAN: On limestone, Mt. Hee-gni-chao, above Hokin (*Delavay*, 82—*co-type*): above Tapintze (*Delavay* in 1885); Nanfantchwang (*Ten*, 299); divide between Hoching and Lankong valleys (*Forrest*, 2779—*type* of *P. langkongensis* *Forrest*, 5976); eastern flank of Lichiang Range (*F.* 10873); mountains N.E. of Yangtze bend (*F.* 10694); Tong Shan in Yangtze bend (*F.* 11117, 16453); mountains of Chungtien plateau (*F.* 12586—*type* of *P. malvacea* var. *intermedia*, 12679); Sung-kwei Range (*F.* 21556); (*McLaren's Native Collector*, 158); (*Rock*, 15199); Chienchuan-Mekong divide (*Forrest*, 23408); Yungpeh (*F.* 30183); Tcha-ho (*Maire*); sine loc. (*M.* 3372).

S.W. SZECHWAN: Muli and surrounding mountains (*Forrest*, 16276, 16795, 20508—*type* of *P. atrotubata*, 21425, 22047, 22436, 30255); (*Rock*, 16121, 16270); (*Ward*, 4351, 4520A, 4521); photograph of *type* (?) of *P. neurocalyx* from Tchen-kéou-tin in N.E. Szechwan (*Farges*, 1365); photo of *type* of *P. Rosthornii* from Nan-chwan, E. Szechwan (*Rosthorn*, 2173); photo of *type* of *P. barybotrys* from below Muli, Szechwan (*Hand.-Mzt.*, 7382).

P. malvacea Franch. var. *alba* *Forrest* in Notes Roy. Bot. Gard. Edin., xiv, 48 (1923); W. W. Sm. and *Forrest*, *ibid.*, xvi, 27 (1928), and in Journ. Roy. Hort. Soc., liv, 19 (1929); Fletcher in Gardening Illust., lxiii, 492, with fig. (1941).

Discovered on the Sung-kwei Range in N.W. Yunnan by *Forrest* in 1922, in open alpine meadows at an altitude of 3300–3700 m. This plant differs only in having white flowers.

In the Edinburgh Herbarium there are the following collections:—

N.W. YUNNAN: Sung-kwei Range (*Forrest*, 21557—*type* of var.); (*Rock*, 25198).

S.W. SZECHWAN: Muti Konka, east of Yalung (*Rock*, 23730, 24288).

P. saturata W. W. Sm. et Fletcher sp. nov.*

This species is known only from two collections, one in flower and one in fruit, made by J. F. Rock in 1932 on Muti Konka, a

* Species affinis *P. bathangensis* Petitm. a qua foliis obovatis vel oblongo-ellipticis (nec reniformibus), petiolis lamina brevioribus, corollae colore saturate aurantiaco satis recedit.

Folia petiolo incluso 6–10 cm. longa, tandem ad 18 cm.; lamina primo

snow range east of the Yalung, Mutirong, Territory of Muli, in south-west Szechwan. It was found in mixed forest at an altitude of over 4000 m., which is decidedly higher than is usual for members of the section *Malvacea*. At first it was identified as *P. bathangensis*, but must be distinguished from that species by the shape of its lamina, by the short petioles, and by the more intense colour of the corolla. There appears also to be a difference in the calyx, which is smaller and much less accrescent in fruit than in *P. bathangensis*. Except for the colour of the corolla it invites comparison with *P. blattariformis* in its general habit and to some extent in its foliage. It has not been in cultivation.

A hairy perennial with a short comparatively stout rhizome. Leaves including the petiole 6–10 cm. long, up to 18 cm. long at fruiting time; lamina 4–6 cm. long, 2–3.5 cm. broad, at fruiting time 10–13 cm. long, 4–6 cm. broad, oblong-elliptic to obovate, rounded at the apex, attenuate to almost rounded at the base, deeply undulate-crenate at the margin, pubescent above, softly hairy below, the hairs longer and more numerous along the main veins; midrib and 6–10 pairs of lateral veins slightly impressed above, subconspicuous below; reticulation rather open, usually more or less hidden on the lower surface by the thick covering of hairs; petiole 2.5–5 cm. long, conspicuously pilose, winged and sheathing towards the base. Scape 18–20 cm. long at flowering time, up to 40 cm. at fruiting time, sturdy and erect, pilose, carrying a 10–15-flowered raceme; bracts 5–8 mm. long, lanceolate, pilose; pedicels 5–10 mm. long, pilose, thickening and suberect at fruiting time. Calyx 8–10 mm. deep, 10–15 mm. wide at the apex, broadly campanulate, markedly pilose and covered with sessile amber glands, prominently veined, cut to the middle into broadly triangular lobes only a little accrescent and more or less erect at fruiting time. Corolla deep orange, annulate, heteromorphic; tube twice the

4–6 cm. longa, 2–3.5 cm. lata, obovata vel oblongo-elliptica, apice rotundata, basi angustata vel nunc fere rotundata, bene undulato-crenata, supra pubescens, infra molliter pilosa; petiolus 2.5–5 cm. longus, dense pilosus. Scapus 18–20 cm. altus, fructu ad 40 cm. elongatus, pilosus, racemum 10–15-florum gerens; bracteae 5–8 mm. longae, lanceolatae, pilosae; pedicelli 5–10 mm. longi. Calyx 8–10 mm. altus, apice 10–15 mm. latus, late campanulatus, dense pilosus atque glandulosus, ad medium in lobos late triangulares divisus, tandem in fructu paululum accrescens. Corolla saturate aurantiaca, annulata, heteromorphica; tubus calycem duplo superans, anguste cylindricus; limbus 2.5 cm. diametro lobis obcordatis emarginatis. Stamina in floribus longistylis ad medium tubum corollinum inserta. Stylus longus vix ad annulum pertinens. Capsula subglobosa, tubo calycis inclusa.

WEST CHINA: On Muti Konka, S.W. Szechwan (*J. F. Rock*, 23681—*type*, 24293).

length of calyx, narrowly cylindrical, ampliate above insertion of stamens; limb about 2.5 cm. in diameter with obcordate, emarginate lobes. Stamens, with anthers 1.5 mm. long, attached near middle of corolla-tube in pin-eyed flowers. Long style barely reaching the annulus. Capsule 5–7 mm. long, subglobose, dehiscing by longitudinal valves. Seeds very similar in size, shape and markings to those of *P. bathangensis*.

Represented in the Edinburgh Herbarium by the following:—

S.W. SZECHWAN: Muti Konka, east of Yalung (*Rock*, 23681—*type*, 24293).

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THE GENUS PRIMULA: SECTION PYCNOLOBA Balf. f.

By W. WRIGHT SMITH and H. R. FLETCHER.

(Read 18th May 1944.)

There is but one representative of this section, the peculiar even bizarre species *P. pycnoloba*, which presents a facies in its inflorescence quite unlike that of any other *Primula*. It has been said that only dissection would afford convincing proof that it really is a *Primula*. In the original description Bureau and Franchet pointed out that the characters of its foliage recall closely those of *P. malvacea*. In his Monograph Pax (*l.c.*, 23) had to rely on the previous description in default of specimens and allocated the plant aptly enough to his broadly defined section *Sinenses*. In 1913 Balfour (*l.c.*, 144) considered *P. pycnoloba* to stand by itself amongst *Primulas* on account of its curious calycine evolution and thus entitled to separate sectional status. Craib (*l.c.*) believed that there are good reasons for this view, which is accepted also by Smith and Forrest (*l.c.*, 37). The cytological evidence (Bruun, *l.c.*, 29) is on the whole in support but emphasises the undeniable affinity of the *Primulas* of the Paxian section *Sinenses*. In general then, the position of section *Pycnoloba* is in proximity to such sections as *Malvacea* and *Cortusoides*. It is clearly in that kinship, but cannot be allocated to either of these sections nor to any other cognate one. Its distinguishing features are the contracted racemose inflorescence, forming a rounded mass as broad as long, the huge calyx, the very small corolla and also the relatively small size of the corolline lobes. The above references and further details will be found under the description of the solitary species.

P. pycnoloba Bur. et Franch. in Morot, Journ. de Bot., v, 99 (1891); Pax in Engl. Pflanzenr. Primulaceae, 23 (1905); Journ. Roy. Hort. Soc., xxxviii, Proc., p. cxxiv (1912); Balf. f., *ibid.*, xxxix, 137, 144, fig. 47 (1913); Craib in Bot. Mag., t. 8612 (1915); Farrer, Engl. Rock Gard., ii, 174, pl. 19 (1919); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 37 (1928), and in Journ. Roy. Hort. Soc., liv, 18, fig. 58 (1929); Bruun, Cytological Studies in *Primula*, 29, 125 (1932); Cooper in New Fl. and Silva, v, 185 (1933).

This remarkable species was discovered in 1890 by Prince Henri d'Orléans and his companion M. Bonvalot and the locality given is the neighbourhood of Tatsienlu in Western Szechwan. The type material is in the Paris Herbarium. In the original description Bureau and Franchet call attention to the striking contrast between the calyx and the corolla. In the genus no other species can be mistaken for it. It is well represented in the Botanical Magazine (*l.c.*). The next record of its finding is in 1906 when E. H. Wilson collected it, again near Tatsienlu, and also secured seeds which brought it into cultivation. It still persists in a few gardens in this country. More information is needed as to its distribution in Szechwan. It appears to be somewhat uncommon and travellers in that province during the last forty years have only rarely reported its occurrence. Particularly would it be of interest to know *where* in the Tatsienlu region it does occur and in what quantity, for keen collectors of *Primula* such as Cunningham were resident in that city for many years and did not find it. Harry Smith gives the elevation of 1900–2000 m. for the plants he found in 1934 in meadows at Hualinpin. The species is said to “thrive well under ordinary alpine treatment in a shaded portion of the Rock Garden,” but it can only too readily be lost. There is apparently no record of its setting seed in culture and it is usually propagated by root-buds, “which afford a ready means.” In some hands no doubt true.

A more or less robust hairy perennial spreading by means of rootbuds. Leaves including the petiole 6–25 cm. long; lamina 5–15 cm. long and broad, broadly ovate to suborbicular, deeply cordate at the base, crenate-lobulate to lobulate at the margin, the lobules minutely and irregularly denticulate, dark green, bullate and pubescent or pilose above, paler green below and markedly hirsute especially along the main nerves and thinly covered with whitish or amber sessile glands; nerves impressed above, midrib and 4–5 pairs of lateral nerves conspicuous below; petiole 2–15 cm. long, stout, copiously white- or pinkish-lanate, vaginate at the base. Scape 8–20 cm. long, markedly lanate, sturdy and erect but towards the apex recurving and there carrying a many-flowered contracted raceme forming a more or less round inflorescence about as broad as long and 5–7 cm. in diameter; bracts 7–20 mm. long, 3–5 mm. broad, lanceolate to oblanceolate, entire or faintly serrulate, villous, pale yellowish-green; pedicels 5–15 mm. long, villous. Calyx 15–25 mm. long, 25–30 mm. wide at the apex, widely campanulate, pale yellowish-green, villous,

cut to the middle or even more into lanceolate acute entire or faintly denticulate ciliate lobes each with one prominent main nerve and a pair of subprominent lateral nerves. Corolla with a dark-red to bright violet limb, yellowish-green tube and eye, exannulate, heteromorphic; tube about 13-15 mm. long, cylindrical, ampliate above the insertion of the stamens, sometimes slightly hairy without; limb 7-8 mm. in diameter with more or less oblong slightly emarginate lobes. Stamens, with anthers at most 1 mm. long, inserted near middle of corolla-tube in pin-eyed flowers. Long style as long as or almost as long as corolla-tube.

The species is represented in the Edinburgh Herbarium by the following:—

SZECHWAN: Hualinpin (*Harry Smith*, 10353). Cultivated material from the Royal Botanic Garden, Edinburgh.

THE GENUS PRIMULA: SECTION DRYADIFOLIA Balf. f.
By W. WRIGHT SMITH and H. R. FLETCHER.

(Read 18th May 1944.)

The dominant species in this small section is *P. dryadifolia*, described by Franchet (1) in 1884 from material collected by Delavay in the previous year on the Lichiang Range in Yunnan. In a brief comment at the end of his diagnosis Franchet compares the species with *Dryas octopetala* in its very similar facies and states that it is well characterised by its leaves and by the shape of its bracts. As for its position in the genus, he would place it by the side of *P. uniflora*. In 1889 Pax (2) in his exposition of the sections of Primula included it within his Callianthae, judging it to be a link between that section and Cordifoliae. But in 1905 when Pax (3) published his Monograph, he adopted Franchet's suggestion and kept it in company with *P. uniflora* and thus in his section Soldanelloideae. No further material, however, had in the meantime become available and the data given by Franchet were repeated. But in the next thirty years ample gatherings were made. Forrest (4) collected the plant in 1905 and gave a description of it under *P. congestifolia* in 1908. In an article, however, written by Forrest (5) in 1911 he makes it clear that his plant can be no other than *P. dryadifolia*. He also secured seed, but the resultant plants were not sufficiently advanced to be exhibited in flower at the Primula Conference in 1913. At that Conference Balfour (6) (*l.c.*, 165) proposed a section Dryadifolia, giving no diagnosis but citing *P. dryadifolia* as the solitary member. "I have not yet satisfied myself regarding the right position of *P. dryadifolia* Franch.—one of the finest of Primulas. . . . The habit of the plant is altogether foreign to plants in the Soldanelloid group. The suffruticose habit takes one to Suffruticosa. But the leaves in *P. dryadifolia*, as well as the second sessile large drooping flowers, seem to forbid the association. In the circumstances I sit on the fence until study of the living plant gives more data and I place it here after the group I have just dealt with (Yunnanensis) because we may yet find links indicating a relationship. . . . At Edinburgh we have young plants in their third year of growth." Meanwhile in 1911 *P. Jonarduni* (7) was described from the East Himalaya, but without any suspicion of its close kinship with

P. dryadifolia. In 1915 appeared *P. philoresia* (8), later to be deemed a dwarf state of *P. dryadifolia*, and in 1916 *P. oreina* (9), ascribed to section Bella but now recognised to be equivalent to *P. Jonarduni*. In 1920 Balfour (10) published as members of the section *P. chrysophylla*, *P. cyclophylla*, and *P. mystrophylla*, but in none of these descriptions did he express any further views on the position of his section. At the Primula Conference of 1928 Smith and Forrest (11), dealing with the sections of the genus, gave a brief note on *Dryadifolia* and stated its content and its position in the key to the sections. It will facilitate reference to their views if the apposite part of their note is quoted: "This section is a somewhat isolated one. Its habit recalls the *Bullatae* section, but its foliage and flowers are very different. Some of its smaller members such as *P. triloba* invite comparison with section Bella and have been associated with that section. The corolla-tube and throat are sometimes hairy, but the characteristic pompon of Bella is absent. We regard it rather as a suffruticose parallel to *Minutissimae* and Bella and cannot favour the view of Franchet, adopted by Pax, of relegating it to section *Soldanelloideae*. The head of flowers and the bracts of its larger members are certainly suggestive of *Soldanelloideae*, but the leaves and the flower-structure are quite alien to that section. The massive rhizomes covered with the remains of many leaves mark the section easily from all the sections except *Bullatae*." To the above extract may be appended a comment by Stapf (12): "*P. dryadifolia* is a member of a small section of *Primula* . . . whose exact affinity is still doubtful."

Before any conclusion is attempted, the following points can be dealt with. *P. bella* and its associates are no longer the only species with the characteristic pompon, for the same structure appears in *P. Tsongpenii* which is clearly within *Dryadifolia*. But this link is not to be neglected. Of interest is the position of *P. triloba* placed in Bella by Balfour, but transferred to *Dryadifolia* by Smith and Forrest. A review of its features argues rather its inclusion in *Minutissimae* along with *P. muscoides*, *P. reptans*, and *P. tenuiloba*, but it is retained in *Dryadifolia* temporarily as a matter of convenience (see under *P. triloba*, p. 145). These differences of opinion, however, indicate the proximity of the sections concerned. Further evidence of this is shown if a comparison is made between the mat-formations of *P. reptans* and *P. mystrophylla*. The section *Dryadifolia* can therefore be assessed, not as a suffruticose parallel to *Minutissimae*, but rather as a near relation of it. To some extent their geographical areas overlap. Presumably

Dryadifolia with stout and often woody rhizomes is the older type, but in matters phyletic it is easy to speculate. The link with *Minutissimae* (which includes *Bella*) brings *Dryadifolia* almost within the range of *Farinosae*, but no bridging species present themselves.

The general character of the section is adequately represented in the account given later of *P. dryadifolia* itself, but the distinctive marks can be thus stated: The woody rhizomes clothed with withered leaves as seen in *Bullatae* and *Auricula*; the cushion-like growth-form; the evergreen crowded leaves of ovate to orbicular outline with crenulate recurved margins and of peculiar consistency; the few-flowered inflorescence; conspicuous hooded bracts; flowers as large as the leaves, sessile or subsessile; corolla annulate with emarginate lobes; capsule not exceeding the calyx.

The most widespread species and the most vigorous is *P. dryadifolia*. It would not be amiss to regard the other species (except *P. triloba*) as derivatives from it. The area of distribution includes the western ranges of Yunnan and Szechwan, the Bhutan and Assam Himalaya, the adjoining alps of south and south-eastern Tibet, and a corner of N.W. Burma. It thus occupies much the same territory as subsection *Bella* in the *Minutissimae*. The species are all high alpine with an altitudinal range of 4000–5500 m. The cytology of the section has not been investigated. The species do not take kindly to culture and success has been very limited. *P. dryadifolia* and *P. chlorodryas* have been brought to flowering stage, but at this date it is unlikely that either species survives in Europe.

LITERATURE.

- (1) Bull. Soc. Bot. France, xxxii, 270 (1885).
- (2) Engl. Bot. Jahrb., x, 213 (1889).
- (3) Engl. Pflanzenr. Primulaceae, 67 (1905).
- (4) Notes Roy. Bot. Gard. Edin., iv, 226 (1908).
- (5) Gard. Chron., I, 208 (1911).
- (6) Journ. Roy. Hort. Soc., xxxix, 133, 165 (1913).
- (7) Rec. Bot. Surv. Ind., iv, 269 (1911).
- (8) Notes Roy. Bot. Gard. Edin., ix, 34 (1915).
- (9) *Ibid.*, ix, 189 (1916).
- (10) *Ibid.*, xiii, 6, 9 (1920).
- (11) *Ibid.*, xvi, 22 (1928).
- (12) STAPP in Bot. Mag., t. 8902 B (1938).

KEY TO THE SPECIES.

A. Leaves crenate but not lobed: corolla annulate, glabrous without:

B. Flowers purplish-rose:

C. Flowers carried above leaves on distinct scapes; corolla-tube glabrous or subglabrous within

dryadifolia

- CC. Flowers more or less immersed in leaves, often solitary;
corolla-tube usually hairy within:
D. Leaves efarinose below; corolla-throat with pompon of hairs *Tsongpenii*
DD. Leaves farinose below; no pompon in corolla-throat:
E. Petiole widely winged, subequal to lamina; corolla-tube hairy within *Jonarduni*
EE. Petiole very slender, 2-3 times the lamina; corolla-tube glabrous within *mystrophylla chlorodryas*
BB. Flowers yellow *triloba*
AA. Leaves trilobed; corolla exannulate, glandular-pilose without .

P. chlorodryas W. W. Sm. in Notes Roy. Bot. Gard. Edin., xvi, 223 (1932); Gard. Chron., xcvi, 208, fig. 85 (1934); Journ. Roy. Hort. Soc., lix, Proc., p. clxxxii (1934); *ibid.*, lxi, 257, Proc., p. clxii (1936).

This plant is known only from the Fuchuan Range which lies to the south-west of Wei-Hsi, on the Mekong-Salwin divide, where it was discovered by Rock in 1928. This locality is very close to the meeting place of Yunnan, Burma, and Tibet. Rock records it as growing on alpine limestone boulders at 4450 m. The four subsequent gatherings quoted below are entirely consistent with the type. The affinity of *P. chlorodryas* is clearly with *P. dryadifolia* from which it differs in the yellow flowers with the corolla-tube villous within. Seed was obtained in 1932, and living plants in flower were exhibited by Lord Aberconway at the May meeting of the Royal Horticultural Society in 1934. Later in the same year the species bloomed in several gardens, raised from seed collected by Rock and also by Forrest. It proved a difficult plant to retain in cultivation, and at this date does not survive in Edinburgh and apparently not elsewhere.

An evergreen farinose plant forming small compact cushions, with a long thin rhizome covered by leaf scars and the withered remains of old foliage. Leaves of firm texture clustered together at the apex of the rhizome, 1.5-3 cm. long including the petiole; lamina 5-15 mm. long, 5-10 mm. broad, ovate to oblong-elliptic, rounded at the apex, rounded or broadly cuneate at the base, crenate and recurved at the margin, efarinose but with farinipotent glands above, bright yellow-farinose below; midrib conspicuous below; lateral nerves and reticulation obscure; petiole subequal to or slightly longer than lamina, prominently winged, sheathing towards base. Scape 3-8 cm. tall, slender, farinose, carrying 1-3 flowers; bracts 5-7 mm. long, 4-5 mm. broad, broadly ovate, green and tinged with purple, rounded or obtuse at apex, with one prominent nerve, farinose, ciliolate at margin; pedicels almost

obsolete or 1–2 mm. long, copiously farinose. Calyx 6–10 mm. long, campanulate, sparingly farinose without, often purple-tinted, conspicuously 5-veined, cut to about the middle into ovate to oblong-ovate lobes, rounded or obtuse at the apex. Corolla pale yellow, annulate, heteromorphic; tube a little longer than calyx, occasionally nearly twice as long, cylindrical, ampliate above insertion of stamens, hairy within: limb 1.5–2 cm. in diameter with $\pm$ patent obcordate deeply emarginate lobes. Stamens, with anthers 1.5 mm. long, inserted towards apex of corolla-tube but not reaching annulus in thrum-eyed flowers, towards base of tube in pin-eyed. Long style reaching to within 1 mm. of annulus; short style 1–1.5 mm. long. Capsule cylindrical, as long as or slightly longer than calyx, dehiscing by longitudinal valves. Seeds 1–1.25 mm. in diameter, disc-like with rounded to oval outline, grossly vesicular-surfaced at margin.

The species is represented in the Edinburgh Herbarium by the following specimens:—

N.W. YUNNAN: Mount Fuchuan, Mekong-Salwin divide (*Rock*, 17027—*type*, 22750, 23257); (*Forrest*, 30232); (*McLaren's Native Collector*, 135).

P. dryadifolia Franch. in Bull. Soc. Bot. France, xxxii, 270 (1885); Pax in Engl. Bot. Jahrb., x, 213 (1889), and in Engl. Pflanzenr. Primulaceae, 67 (1905); Hemsl. in Journ. Linn. Soc., xxvi, 38 (1889); Forrest in Gard. Chron., l, 208, fig. 100 (1911), and in Journ. Roy. Hort. Soc., xli, 207 (1915); Balf. f., *ibid.*, xxxix, 133, 165 (1913); Kingdon Ward, Mystery Rivers of Tibet, 64 (1923), and Romance of Plant Hunting, 157 (1924); Hand.-Mzt., Naturbild. Südwest China, 90 (1927), and in Symb. Sin., vii, 741 (1936), and in Journ. Roy. Hort. Soc., liv, 59 (1929); W. W. Sm. and Forrest, *ibid.*, liv, 28, fig. 25 (1929), and in Notes Roy. Bot. Gard. Edin., xvi, 22 (1928); Stapf in Bot. Mag., t. 8902 B (1938). *P. dryadifolia* subsp. *congestifolia*, *chrysophylla*, and *cycliophylla* W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 22 (1928), and in Journ. Roy. Hort. Soc., liv, 28 (1929). *P. congestifolia* Forrest in Notes Roy. Bot. Gard. Edin., iv, 226, t. 28 (1908). *P. philoresia* Balf. f., *ibid.*, ix, 34 (1915). *P. chrysophylla* Balf. f. et Forrest, *ibid.*, xiii, 6 (1920). *P. cycliophylla* Balf. f. et Farrer, *ibid.*, xiii, 9 (1920).

This very beautiful species was one of the discoveries of Abbé Delavay who collected it in July 1884 on the Lichiang Range in

Western Yunnan, at 4000 m., near the glacier and the perpetual snow. An account of its habitat is given by Forrest (*l.c.*, 208) who has recorded it as growing abundantly on huge limestone screes up to 5500 m. The original specimens (in the Paris Herbarium) were described by Franchet who made no particular mention of the peculiar character or of the beauty of this *Primula*, but very aptly compared it with *Dryas octopetala* in habit and assigned it a place near the Himalayan *P. uniflora*. From 1905 onwards it has been frequently collected and is now known to be widely distributed, as the citation of specimens below clearly indicates. In its extensive area it has colonised not only limestone but also gneiss and granite and exhibits considerable variety in growth forms. Some of these may be nothing but responses to transitory conditions in the environment, but others have in the past invited specific separation. The ample material now available favours the inclusion as synonyms of the following three names which, however, merit a passing note. *P. chrysophylla* is a form with vivid yellow farina, instead of the white of Delavay's original. *P. cyclophylla* described from Burmese specimens is found also in Tibet and Yunnan in company with the typical *P. dryadifolia* and can be regarded as a form with small orbicular leaves. *P. congestifolia* is a densely matted state from the Mekong-Salwin divide. Seed of the species, obtained chiefly by Forrest, was available in 1911 and subsequent years, and plants flowered at Edinburgh and elsewhere in 1914. The plants, however, did not take kindly to culture and it was difficult for them to attain to the stout rhizomic development which is their marked characteristic in their native haunts. The individual plants were consequently short-lived, but further accessions of seed kept the species in cultivation until 1938, beyond which date there is silence. The plants which grew for a time displayed the beauty of the flower, but failed to do justice to this remarkable *Primula* which could not be induced under garden conditions to emulate the wide cushions of *Dryas*.

An evergreen cushion-plant at most 10 cm. high with a long stout rhizome forming numerous leafy branches with contracted internodes and covered below with the overlapping withered remains of old foliage. Leaves varying much in size and shape according to the degree of inrolling of the margin, including the petiole 1.5–5 cm. long; lamina 0.5–2 cm. long, 0.3–1.3 cm. broad, broadly ovate or broadly elliptic to suborbicular, rounded or obtuse at the apex, truncate or occasionally cordulate or broadly cuneate at the base, crenate and usually tightly recurved at the margin, coriaceous,

sprinkled above with farinipotent hairs, densely covered below with white or yellow farina; midrib broad and conspicuous; lateral nerves visible under the farina; petiole subequal to or nearly twice as long as the lamina, broadly winged throughout, sheathing towards the base, sparingly farinose. Scape 1-10 cm. tall, slightly arcuate, pubescent, sparingly farinose towards the apex, carrying 1-5 flowers: bracts 5-12 mm. long, 3-7 mm. broad, oblong-ovate or broadly ovate to elliptic, obtuse, often coarsely and irregularly toothed at the apex, dull blackish-purple, minutely puberulous and faintly mealy without, slightly more mealy within; pedicels obsolete or nearly 2 mm. long, in fruit up to 3 mm. long. Calyx 7-12 mm. long, broadly campanulate, minutely puberulous, farinose at the base, suffused with purple, cut to the middle into ovate to oblong-ovate lobes rounded or obtuse at the apex. Corolla rose-crimson with a darker eye or else a lighter or greenish-yellow eye, annulate, heteromorphic; tube as long as the calyx or half as long again, cylindrical, ampliate above insertion of stamens, glabrous without, glabrous or faintly puberulous within; limb 1.5-2.5 cm. in diameter with obcordate bilobulate lobes, the lobules entire or 2-3-dentate. Stamens, with anthers 1.5 mm. long, inserted at apex of corolla-tube and reaching annulus in some thrum-eyed flowers but only two-thirds up the tube in others, just below the middle of corolla-tube in some pin-eyed but much lower in others. Long style a little more than half the length of the corolla-tube or up to the annulus. Short style one-third to one-half the length of tube. Capsule as long as calyx, oblong-ovoid, opening with short erect subacute or blunt teeth. Seeds 1-1.5 mm. in diameter, somewhat flattened or disc-like, rounded or oval or subquadrate, grossly vesicular-surfaced.

Represented in the Edinburgh Herbarium by the following collections:—

YUNNAN: Lichiang Snow Range (*Delavay* in 1884—*co-type*); (*Forrest*, 6142, 16958, 30319); (*Yü*, 15249); (*Rock*, 24895); Mountains of the Chungtien plateau (*Forrest*, 12729); (*Yü*, 13659); Chungtien (*Hand. - Mzt.*, 6917); Mountains N.E. of Chungtien (*Forrest*, 16506, 16959); Mekong-Salwin divide (*F.* 14090, 19730, 20351, 20726); Mount Fuchuan (*F.* 30230); (*Rock*, 17032, 22723, 23277); Atuntze (*Ward*, 798—*type* of *P. philoresia*, 86); Mountains N. of Atuntze (*Forrest*, 14070, 14106, 19759, 20173, 22964); Chien-chuan-Mekong divide (*F.* 22361); Mekong-Yangtze divide (*F.* 14825); Chinsa Shan (*F.* 30298); Haba Shan (*Rock*, 24779, 25307); Yulung Shan (*R.* 25324); Motung Shan (*R.* 23335); Pei-ma Shan (*R.* 22830);

Hung Po (*R.* 22893); sine loc. (*Forrest*, 11342, 15007, 15160, 15337).

SZECHWAN: Muli Mountains (*Forrest*, 16496, 16594—*type* of *P. chrysophylla*); Mount Konka, Risonquemba, Konkaling (*Rock*, 16371); Mount Mitzuga, west of Muli Gomba (*R.* 16593); Grasslands of Yulong-Hsi, south of Tatsienlu (*R.* 17481); Mountains north of Baurong and east of the Yalung River (*R.* 17778); Mount Yara, near Tatsienlu (*Harry Smith*, 11615).

S.E. TIBET: Mekong-Salwin divide (*Forrest*, 478—*type* of *P. congestifolia*); Dokar La (*F.* 14302); Londre Pass (*F.* 19765); Salwin-Kiu-chiang divide (*F.* 20273, 20743); Mount Kaakerpo (*Rock*, 22960); Mount Kinichumpo, Upper Salwin River (*R.* 22180, 22181, 22539, 22551); Doshong La (*Ward*, 5837); Nyima La (*W.* 5813); Kechen La, near Tsona (*Ludlow and Sherriff*, 671); Mago (*L. and S.*, 763); Truka La, Mago (*L. and S.*, 801); Kulu Phu Chu, near Paka (*L., S. and Taylor*, 5952); Mira La, Nyang Chu (*L., S. and T.*, 6154).

BURMA: Western flank of the N'Maikha-Salwin divide (*Forrest*, 26876, 27265); Chimili Alps (*Farrer*, 1183—*type* of *P. cyclophylla*); Chawchi Pass (*Farrer*, 1885).

BURMA-TIBET FRONTIER: Seinghku Wang (*Ward*, 7080).

P. Jonarduni W. W. Sm. in *Rec. Bot. Surv. Ind.*, iv, 269 (1911); Craib in *Journ. Roy. Hort. Soc.*, xxxix, 189 (1913); W. W. Sm. and *Forrest*, *ibid.*, liv, 28 (1929), and in *Notes Roy. Bot. Gard. Edin.*, xvi, 22 (1928); *Sherriff and Taylor* in *Quart. Bull. Alp. Gard. Soc.*, vii, 237, fig. p. 235 (1939). *P. oreina* Balf. f. et *Cooper* in *Notes Roy. Bot. Gard. Edin.*, ix, 189 (1916).

The discovery of this species was made in June 1905 by Mr. J. C. White, at that time Political Officer in Sikkim, while on a tour in Bhutan. Comparison with the Indian material of the genus at Calcutta and at Kew showed that the plant was very distinct from anything recorded from the Himalaya, and in the original description the only suggestion for its affinity is an approach to the *Farinosae*. Its relationship with the then rare *P. dryadifolia* was not suspected, and it still remains the only representative of the section from the Indian Himalaya. It grows in mat-like formations on mossy boulders or on cliff-ledges at 4000–5300 m. It has therefore to endure the same extreme conditions as *P. mystrophylla*, found farther to the east, from which it differs in the shape of the leaves and petioles, as also in the pilose interior of the corolla-tube. The habit of the plant is well shown in the figure given by *Sherriff and Taylor* (*l.c.*) who state: "It grows in more or less open rock

crevices, seaming the cracks with its leafy crowns which conceal the copious withered foliage of previous years." There is no record of the species in cultivation.

A small evergreen farinose plant with a comparatively stout rootstock from the apex of which spread many branches densely clothed for a time with the withered remains of old foliage. Leaves clustered on the branches, 8–20 mm. long including the petiole; lamina 4–10 mm. long, 4–8 mm. broad, ovate to oblong-ovate, rounded at the apex, rounded or even faintly cordate at the base, crenate but with the crenations so reflexed that the margin appears entire, coriaceous, glabrous above, yellow- or white-farinose below; midrib slightly impressed above, prominulent below; lateral nerves obscure; petiole equal or subequal to the lamina, broadly winged, sheathing at the base. Scape usually about 5 mm. long, hidden among the foliage, occasionally 1–2 cm. long and then raised above the leaves, farinose, commonly 1-flowered, occasionally 2-flowered; bracts 4–7 mm. long, 3–5 mm. broad, ovate to ovate-lanceolate, cucullate, rounded at the apex, faintly farinose without, more copiously within; pedicels obsolete or at most 1 mm. long. Calyx 6–8 mm. long, campanulate, sometimes deeply stained with purple, sprinkled with farina without, farinose especially at the base within, cut to the middle or almost so into ovate to elliptic lobes, rounded or obtuse at the apex. Corolla rose-crimson or magenta with a dark purple or even a white eye, annulate, heteromorphic; tube as long as or a little longer than the calyx, cylindrical, ampliate above insertion of stamens, hairy within; limb 1–2.5 cm. in diameter with obcordate deeply emarginate lobes. Stamens, with anthers 1.5 mm. long, inserted 1.5–2 mm. above base of tube in pin-eyed flowers, a little above middle of tube in thrum-eyed. Long style as long as calyx; short style 1.5–2 mm. long. Capsule as long as calyx dehiscent by longitudinal valves. Seeds 1 mm. in diameter, resembling those of *P. dryadifolia*.

The species is represented in the Edinburgh Herbarium by the following collections:—

BHUTAN: Bod La (*J. C. White*, 69—*co-type*); Narim Thang, Kurted (*Cooper*, 4247—*type* of *P. oreina*); Singhi, Kurted (*C.* 4973); Me La (*Ludlow and Sherriff*, 386); Marim Thang, Kang La (*L. and S.*, 485).

S. and S.E. TIBET: Bimbi La (*Ludlow and Sherriff*, 1805); Mipa, Tsari (*L. and S.*, 2181); Langong Chu (*L., S. and Taylor*, 3917); Kuchu La, nr. Paka (*L., S. and T.*, 5932); Doshong La (*Ward*, 5837, 5838); Nyima La (*W.* 5813); Tse Gar (*W.* 11940).

P. mystrophylla Balf. f. et Forrest in Notes Roy. Bot. Gard. Edin., xiii, 14 (1920); W. W. Sm. and Forrest, *ibid.*, xvi, 22 (1928), and in Journ. Roy. Hort. Soc., liv, 28 (1929); Hand.-Mzt., *ibid.*, liv, 60 (1929), and in Symb. Sin., vii, 742 (1936).

This species is a native of the frontier region between the Tibetan province of Tsarong and the extreme N.W. corner of Yunnan. It was found by Forrest in 1917 growing on moist rocks, on crevices of cliffs and screes at 4600–5000 m. The specific name calls attention to the spoon-shaped leaves which have a very small lamina. The habit of the plant suggests extreme alpine conditions, but in the same area and at the same elevation occurs *P. dryadifolia*, differing in no respect from the typical form of the Lichiang Range. It is therefore unlikely that *P. mystrophylla* can be construed as an extreme environmental state of *P. dryadifolia* from which it differs in the slender rhizomes, in the distinctive leaves with elongate petiole, and in the escapose and usually solitary flowers. Another ally is the Himalayan *P. Jonarduni* which deviates in the leaf-form, in the short petioles, and in the hairy interior of the corolla-tube.

Seeds of *P. mystrophylla* were secured by Forrest in 1918, but there is no record of any success in culture.

A caespitose evergreen plant forming cushions 15–30 cm. in diameter and with numerous fibre-like radiating branches up to 15 cm. long which root towards the base and are thickly clothed with the withered remains of old foliage. Leaves including the petiole 1–2 cm. long; lamina 3–8 mm. long and broad, ovate or elliptic to orbicular, rounded at the apex, rounded or truncate or cordulate at the base, crenate, sometimes obscurely so, at the margin with the crenations often recurved, coriaceous, farinose above, thickly covered below with bright yellow farina; nerves apart from the midrib $\pm$ obscure; petiole 2–3 times the lamina, glandular-puberulous, markedly winged, amplexicaul towards the base. Scape 4–8 mm. long, stiff, erect, hidden among the foliage, farinose, sometimes sparingly so, carrying a single flower, occasionally 2–3; bracts 5–6 mm. long, 3–4 mm. broad, usually a pair, broadly ovate, obtuse or rounded at the apex, farinose, keeled; pedicels 1–2 mm. long, enclosed in the adpressed bracts. Calyx 5–7 mm. long, campanulate, slightly farinose, usually stained with purple, cut to the middle into oblong or elliptic-ovate ciliolate lobes, rounded or obtuse at the apex. Corolla deep carmine-rose with a yellow eye, annulate, heteromorphic; tube $1\frac{1}{2}$ –2 times the calyx, cylindrical, ampliate above insertion of stamens, glabrous within; limb 1.5–2 cm. diameter with patent obcordate deeply emarginate lobes. Stamens,

with anthers 2 mm. long, inserted in upper half of corolla-tube in thrum-eyed flowers, towards base of tube in pin-eyed. Long style 1-1½ times the calyx; short style 2 mm. long. Capsule broadly oblong, as long as calyx, dehiscing by longitudinal valves. Seeds 1-1.25 mm. in diameter, rounded or oval or subquadrate discs, surfaced as in *P. dryadifolia*.

Represented in the Edinburgh Herbarium by the following collections:—

S.E. TIBET: Tsarong, on Ka-gwr-pu, Mekong-Salwin divide (*Forrest*, 14221—*type*, 16766, 17244); Tsarong, Salwin-Kiu-chiang divide (*F.* 18895).

YUNNAN: Mekong-Salwin divide (*Forrest*, 14353).

P. triloba Balf. f. et *Forrest* in *Notes Roy. Bot. Gard. Edin.*, xiii, 21 (1920); W. W. Sm. and *Forrest*, *ibid.*, xvi, 22 (1928), and in *Journ. Roy. Hort. Soc.*, liv, 28 (1929).

This dwarf species was discovered by *Forrest* in 1918 in that part of S.E. Tibet which touches on the extreme N.W. corner of Yunnan and so near the frontier that it may well occur also within the Chinese province. In the original description it is associated with *P. bella* and allied species. This placing of it is certainly near the mark, but *Smith* and *Forrest* (*l.c.*) transferred it to section *Dryadifolia* with which it has also a degree of affinity. A detailed analysis leads us to the conclusion that the evidence is mainly in favour of its inclusion in the *Minutissimae*, in company with *P. reptans*, *P. muscoides*, and *P. tenuiloba*. In that assemblage and also in *Dryadifolia* it is readily distinguished by the consistently trilobed leaves. The flower structure recalls that of *P. bella* and of *P. moscophora*, but the corolla-throat, though it is pilose, has no distinct pompon. The habit, the solitary flowers, and the small size and consistency of the leaves invite comparison with *P. mystrophylla* from almost the same area. *Forrest* records his plant as growing on peaty pasture, on screes and on ledges of cliffs at 4600-5000 m. It has not been in culture.

As a recent account of the section *Minutissimae* has been published in *Trans. Bot. Soc. Edin.*, xxxiii, 227 (1942), it may be permitted to retain *P. triloba* within *Dryadifolia* temporarily—with a recommendation that it be transferred to *Minutissimae* in any future summation of species.

A dwarf efarinose plant at most 3 cm. tall including the erect flower, forming cushions 5-10 cm. across, with numerous short branches compacted together and clothed with the withered remains

of old foliage. Leaves including the petiole 6–8 mm. long; lamina 3–4 mm. long and broad, rounded at base, divided to the middle into 3 ovate lobes which are obtuse or rounded at the apex, thinly covered with potentially farinose glands, somewhat fleshy, glabrous; nerves obscure; petiole subequal to the lamina, prominently winged and sheathing at the base. Scape 3–5 mm. tall, stiff and erect, hidden among the foliage, glandular-pilose, carrying 1 flower; bracts solitary, 3–4 mm. long, linear, 1-nerved, glandular-pilose. Calyx 5–6 mm. long, campanulate, densely glandular-pilose, cut to well below the middle into lanceolate acute or acuminate teeth. Corolla rose with a pale yellow or grey-white eye, exannulate, heteromorphic; tube a little longer than or twice as long as the calyx, narrowly cylindrical, ampliate above insertion of stamens, very copiously glandular-pilose without, villous within; limb 1–1.5 cm. in diameter with obcordate deeply emarginate lobes. Stamens, with anthers 1 mm. long, inserted at apex of the corolla-tube in thrum-eyed flowers, about 1 mm. from the base in pin-eyed. Long style as long as corolla-tube; short style about 1 mm. long. Capsule oblong, as long as calyx, dehiscing by longitudinal valves. Seeds 0.5 mm. in diameter, ovoid, obscurely vesicular-surfaced.

Represented in the Edinburgh Herbarium by:—

S.E. TIBET: Tsarong, Londre-Shan (*Forrest*, 16878—*type*); Tsarong, Salwin-Kiu-chiang divide (*F.* 18894).

P. *Tsongpenii* Fletcher in Journ. Linn. Soc., lii, 340 (1942).

This Tibetan species was discovered in 1938 growing at 4600–5000 m. on bare open rocky hillsides. It was found in company with *P. Valentiniana* and *P. Jonarduni*. Its nearest affinity would appear to be the latter species, from which it differs in the conspicuous tuft of hairs in the corolla-throat and in the subfarinose foliage. Between the two there is a close resemblance in habit, in the shape of the small leaves, and in the very short or almost obsolete scape. The same characters exclude it from a near approach to the much more robust *P. dryadifolia* of Western China. The pompon of hairs closing the corolla-tube is of interest and invites comparison with the same structure in *P. bella* and *P. pusilla*. Its presence may well be an indication that in the more slender members of the section *Dryadifolia* there is a degree of relationship with the *Minutissimae*. But from *P. bella* itself and its immediate associates, *P. Tsongpenii* deviates in the leaf-characters, in the suppression of the scape, and in the details of its heterostyly.

Seeds were collected in 1938, but there is no record of any

successful cultivation of the species. The seeds are smaller than in *P. dryadifolia* and the surface markings much less conspicuous.

A dwarf caespitose evergreen and almost completely efarinose plant forming compact mats and with a thin rhizome about 5 cm. long and numerous branches densely clothed with the withered remains of old foliage. Leaves including the petiole 7–10 mm. long; lamina 3–5 mm. long and broad, broadly elliptic to almost rotundate, rounded at the apex, rounded or cordulate at the base, 10–12-dentate and often recurved at the margin, coriaceous, glabrous and efarinose at maturity but with a thin covering of potentially farinose glands below; midrib prominulent with lateral nerves more or less obscure; petiole subequal to the lamina, prominently winged, amplexicaul towards the base. Scape 3–5 mm. long, stiff, erect, immersed in the leaves, speckled with farina, 1-flowered; bracts 3–5 mm. long, broadly ovate or scutiform, ciliolate, minutely farinose; pedicels obsolete or at most 1 mm. long. Calyx 5 mm. long, campanulate, sparsely yellow-farinose, green but tinged with purple, cut to the middle into broadly ovate to oblong lobes rounded or obtuse at the apex. Corolla pink, slightly tinged with purple with a wine-red tube and a lemon-yellow eye, showing a pompon of white hairs at the throat, annulate, heteromorphic; tube $1\frac{1}{2}$ –2 times the length of the calyx, cylindrical, ampliate above insertion of stamens, densely pilose within with long white septate hairs which form the pompon at the throat; limb 1.5–2 cm. in diameter with patent obcordate bilobulate lobes, the lobules being emarginate. Stamens, with anthers about 1 mm. long, inserted near middle of corolla-tube in thrum-eyed flowers, almost at base in pin-eyed. Long style as long as corolla-tube; short style 1 mm. long. Capsule broadly cylindrical, about as long as calyx, dehiscent by longitudinal valves. Seeds 0.5 mm. in diameter, flattened, rounded or oval or subquadrate, vesicular-surfaced.

Represented in the Edinburgh Herbarium by:—

S.E. TIBET: Tsanang La, near Paka (*Ludlow, Sherriff and Taylor*, 5865—*type*); Kucha La, near Paka (*L., S. and T.*, 5931); Lo La, near Molo (*L., S. and T.*, 6554).

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THE GENUS PRIMULA: SECTION CAPITATAE PAX.

By W. WRIGHT SMITH and H. R. FLETCHER.

(Read 18th May 1944.)

The first use of the term Capitatae for a section of the genus *Primula* dates from 1889 when Pax (1) associated seven species under that heading. The pertinent points in his brief diagnosis can be quoted thus: "Folia . . . plus minus rugosa, pilosa, farinosa vel efarinosa, indivisa, dense denticulata. . . . Flores . . . dense capitati, rarius breviter pedicellati, violacei. Bractee . . . basi haud gibbosae. Capsula globosa." His definition received no enlargement in 1905 when the Monograph (2) was published, but five species were added and one, *P. cernua*, removed. It is apparent, however, from his short critical note (*l.c.*, 88) that Pax was not quite satisfied with the homogeneity of his section. He aptly points out that some of the species group themselves round *P. denticulata* and touch on Farinosae, that others such as *P. nutans* and *P. bellidifolia* form a second group approaching section Soldanelloideae, and that *P. capitata* occupies an intermediate position between the two groups. These remarks of Pax foreshadow the subsequent reduction of the contents of the section, for out of his eleven species only *P. capitata* and possibly *P. glomerata* are now regarded as strictly within its confines. The first change was made by Balfour (3) at the third *Primula* Conference in 1913 when he proposed the three sections Muscarioides, Sphaerocephala, and Denticulata, which correspond with the three groups indicated by Pax. In making this alteration Balfour preferred a new term, Sphaerocephala, for the much amended Capitatae. But at the Fourth *Primula* Conference in 1928 Smith and Forrest (4) reverted to the use of Capitatae, but restricted it to *P. capitata* and its subspecies. This is the position taken up in the present review, except for the addition of *P. glomerata* for reasons given in the account of that species.

In sum therefore there appears to be little divergence in opinion. The one point is whether the three groups outlined by Pax are entitled to sectional status; that they are closely akin is admitted. From the cytological point of view it is fortunate that Bruun (5) was able to examine an adequate representation of each section,

and his verdict is clearly in favour of according that status to each. The chromosomes in the three sections are exactly the same size and chiefly the same shape, but each section has a different basic number—in *Capitatae* 9, in *Denticulata* 11, and in *Muscarioides* 10. The ordinary morphological features separating the three sections are not of great moment but suffice. *Capitatae* differs from *Muscarioides* in the non-hairy leaves of harsher texture and usually farinose, in the globular inflorescence, in the shortly stalked but not sessile flowers, and in the greater regularity of structure in calyx and corolla. (These distinctions are discussed more fully in the published account of section *Muscarioides* (6)). The line between *Capitatae* and *Denticulata* is more difficult to draw. In *Denticulata* the flowers are erect, in *Capitatae* pendent. This criterion would be quite satisfactory were it not for the peculiar case of *P. glomerata* which appears to be intermediate between the two sections, favouring *Denticulata* in its erect flowers and *Capitatae* in most of its other features. Between the two sections, however, there is a marked divergence in facies and also in their time of flowering, for *Capitatae* comes into bloom much later in the year. The distribution of the two is very similar, but *Capitatae* is absent from the Western Himalaya. Its range includes Nepal, Sikkim, Bhutan, Southern Tibet, and Western Yunnan.

REFERENCES.

- (1) PAX in Engl. Bot. Jahrb., x, 193 (1889).
- (2) PAX in Engl. Pflanzenr. Primulaceae, 88 (1905).
- (3) BALF. f. in Journ. Roy. Hort. Soc., xxxix, 151, 154 (1913).
- (4) SMITH and FORREST in Notes Roy. Bot. Gard. Edin., xvi, 18 (1928).
- (5) BRUUN, Cytological Studies in *Primula*, 68, 72, 74, 127 (1932).
- (6) SMITH and FLETCHER in Trans. Bot. Soc. Edin., xxxiii, 268 (1942).

KEY TO THE SPECIES.

- | | | | | | | |
|--|---|---|---|---|---|------------------|
| A. Flowers in the capitulum all pendent | . | . | . | . | . | <i>capitata</i> |
| AA. Flowers in the capitulum all $\pm$ erect | . | . | . | . | . | <i>glomerata</i> |

P. capitata Hook. in Bot. Mag., t. 4550 (1850), and in *ibid.*, t. 6916B (1887); Walpers, Ann., iii, 6 (1852–53); Fl. des Serres, vi, t. 618 (1850–51); Cottage Gard., v, 365 (1851); Lem. Jard. Fl., i, t. 80 (1851); Bull. Soc. Tosc. Orbic., iv, 53 (1879); Gartenfl., xxviii, 87, t. 985 (1879); The Garden, xlv, 503 (1894); *ibid.*, lxxvi, 183, with fig., 190 (1912); *ibid.*, lxxix, 124, with fig., 491 (1915); Hook. f. in Fl. Brit. Ind., iii, 486 (1882); Pax in Engl. Bot. Jahrb., x, 193 (1889), and in Engl.

Pflanzenr. Primulaceae, 94 (1905), including var. *typica* Pax and var. *grandiflora* Pax; Nicholson, Illus. Diet. Gard., iii, 218 (1887); Rev. Hort. Belge, xiii, 121 (1887); Journ. Hort., xxxii, 209 (1896); *ibid.*, l, 407 (1905); Watt in Journ. Roy. Hort. Soc., xxix, 298, 302, 305-6 (1904), and *ibid.*, xxxix, 199, 204-7 (1913); Balf. f. in *ibid.*, xxxix, 154 (1913); Craib, *ibid.*, xxxix, 187-188 (1913); W. W. Sm. and Forrest, *ibid.*, liv, 34, fig. 35 (1929); Gould, *ibid.*, liv, 71 (1929); Adamson, *ibid.*, liv, 79 (1929); Mottet, Monogr. Genre Primevère, t. 10 (1910); Farrer, Engl. Rock Gard., ii, 117 (1919); Cox and Taylor, Primulas, 93 (1928); Gard. Chron., l, 294 (1911); *ibid.*, lxxvii, 7 (1925); Balf. f. in Notes Roy. Bot. Gard. Edin., ix, 47, 160, 163, 178, 184, 193 (1915); W. W. Sm. and Forrest in *ibid.*, xvi, 18 (1928); Bruun, Cytological Studies in Primula, 72, 127 (1932). *P. globifera* Griff. Itin. Notes, 148 (1837-38) —nom. nudum.

This well-known species was discovered by Hooker in 1849 in the Sikkim Himalaya. Seed collected by him near Lachen in June, possibly from capsules of the previous year, gave rise to plants at Kew in 1850 on which the elder Hooker based the first description. *P. denticulata* and *P. farinosa* were cited as somewhat akin. In 1882 Hooker (*l.c.*) kept it distinct from *P. denticulata* with great hesitation, but in 1887 (Bot. Mag., 6916B) he figured the species again, calling attention to the "globose densely crowded head of sessile flowers which open slowly, and the uppermost unexpanded ones are depressed and imbricate over one another like the tiles of a house." He refers also to the occurrence of many forms within the species and assesses Bot. Mag., t. 4550, as an extreme form (high alpine ?) with t. 6916B at the other end of the scale in its much larger flowers. In 1889 Pax (*l.c.*) placed it at the head of his new section Capitatae, in which he included six other species, none now regarded as closely akin to it. In 1905 in his Monograph *P. capitata* was divided into two varieties, var. *typica* and var. *grandiflora*, which correspond to the two figures in the Botanical Magazine already referred to. At the Primula Conference in 1913 Craib (*l.c.*, 188) expressed the view that three plants specifically distinct were included in the botanical material placed under *P. capitata*. This aggregate was subsequently analysed by Balfour (*l.c.*, 185) who published in 1916 some six binomials, considered to be microspecies or forms and as such to be retained within *P. capitata* in its wider interpretation. A degree of variation is to be expected, for the species has an area of distribution very similar to that of

P. sikkimensis and almost as extensive. The altitudinal range is normally 4000–5000 m., but the plant may descend sometimes to 3300 m. Environmental factors may well have an influence and deviations from a presumed norm have been noted in the field, in the herbarium, and in the garden. These have been very variously assessed as forms, varieties, or even subspecies. No controlled experiments have, however, been carried out on plants raised direct from seed collected in the wild. Smith and Forrest (*l.c.*, 18) considered the section to consist of one main species and associated with it five subspecies. They comment as follows: "All the described plants of this section can be grouped round *P. capitata* as a centre. They differ somewhat in habit, in degree of mealiness, in the dentation of the leaves, and in size of truss and of flower. These distinctions are observable in the cultivated plants but transitions are numerous." In this review the subspecies are retained as such, with the caveat that they may have been given a higher status than is their due. Yet Farrer (*l.c.*, 117) from his horticultural experience viewed them as allied but quite definite species.

P. capitata has proved amenable in cultivation, seeds freely and has continued as a garden plant since its first introduction.

A sturdy farinose plant with a short usually stout rhizome and devoid of basal bud-scales. Leaves including the petiole 2–13 cm. long, 0.5–2 cm. broad, oblong or oblanceolate to oblong-spathulate, acute to rounded at the apex, tapering at the base into the winged petiole at most subequal to the lamina usually much shorter, denticulate and often recurved at the margin, covered above with farinipotent glands and sometimes with a little farina, generally plastered with white farina below but occasionally only thickly covered with potentially farinose glands; midrib conspicuous with lateral nerves and reticulation impressed above prominent below. Scape 10–45 cm. tall, markedly farinose especially towards the apex, carrying a discoid head of many or few deflexed flowers; bracts often numerous and forming an apical tuft or crown, 6–8 mm. long, 3–4 mm. broad, ovate or broadly lanceolate, acute or sometimes toothed, white-farinose, often stained purple; pedicels subobsolete, at fruiting time at most 1.5 mm. long. Calyx 5–8 mm. long, campanulate, slightly oblique, markedly white-farinose and stained with purple, cut for two-thirds into broadly ovate to elliptic acute or obtuse lobes. Corolla blue-purple to deep purple with a yellow eye, annulate or exannulate, heteromorphic, slightly farinose without; tube only a little longer than the calyx or nearly twice as

long, cylindrical, slightly inflated above insertion of stamens; limb 7–10 mm. in diameter with more or less patent obcordate emarginate lobes. Stamens, with anthers 1–1.5 mm. long, inserted at base of corolla-tube in pin-eyed flowers, just above middle or even higher in thrum-eyed. Long style as long as calyx; short style 1–2 mm. long. Capsule subglobose, included in the calyx, dehiscing by longitudinal valves. Seeds 0.5 mm. in diameter, quadrate-angular to ovoid or subglobose, minutely vesicular-surfaced.

The species is represented in the Edinburgh Herbarium by the following collections:—

SIKKIM: Lachen (*King's Collector* in 1886); Yeumtong (*Gammie* in 1892); Gamothang (*Cave* in 1922); Changu (*Cooper*, 447); (*Hooker* at 10–16,000 ft.).

S. TIBET: Chaerlung, Chumbi Valley (*Ribu and Rhomoo*, 395, 402); Chumolari (*Dungboo* in 1882); below the Ata Kang La, Zayul (*Ward*, 10901).

BHUTAN: Biaka Pumthang (*Cooper*, 4148); Ohra Pumthang (*C.* 4731, 4732); Changsethang, Mungde Chu (*Ludlow and Sherriff*, 3403); Bela La, Paro (*L. and S.*, 3574).

P. capitata Hook. subsp. **Craibiana** (Balf. f. et W. W. Sm.) W. W. Sm. et Forrest in Notes Roy. Bot. Gard. Edin., xvi, 18 (1928), and in Journ. Roy. Hort. Soc., liv, 35 (1929). *P. Craibiana* Balf. f. et W. W. Sm. in Notes Roy. Bot. Gard. Edin., ix, 159 (1916).

This plant deviates from *P. capitata* in the narrower, more strongly erose-denticulate leaves efarinose above but covered below with bright yellow farina, in the globose not discoid head, and in the smaller narrower bracts.

The type in Kew Herbarium was collected by Hooker in 1849. The representation at Edinburgh is:—

SIKKIM: Sheraothang (*Cooper*, 804); Chaethanglaka (*Ribu and Rhomoo*, 5284); Cho La (*King's Collector*, 4482).

S. TIBET: Sunding, Chumbi Valley (*Dungboo* in 1879).

P. capitata Hook. subsp. **crispata** (Balf. f. et W. W. Sm.) W. W. Sm. et Forrest in Notes Roy. Bot. Gard. Edin., xvi, 18 (1928), and in Journ. Roy. Hort. Soc., liv, 35 (1929); Gould, *ibid.*, liv, 71 (1929); Adamson, *ibid.*, liv, 79 (1929); Bruun, Cytological Studies in Primula, 72, 127 (1932). *P. crispata* Balf. f. et W. W. Sm. in Notes Roy. Bot. Gard. Edin., ix, 162,

185 (1916); Cox and Taylor, *Primulas*, fig. facing p. 20 (1928).

P. capitata Hort. in *The Garden*, xvi, pl. cex (1879).

Easily separable from the other Himalayan members of the section by the absence of meal on the leaves. In this respect subsp. *crispata* resembles the Chinese subsp. *sphaerocephala*, but is a more vigorous plant differing in its discoid, not globose, head and in its larger more open flowers.

Represented in the Edinburgh Herbarium by the following:—

SIKKIM: Laghep (*Cooper*, 951—*type*); Kanglasa (*Cave* in 1919); Karponang (*Cave* in 1910 and 1917); *sine loc.* (*Cave*, 7055).

BHUTAN: East Tashigong ridge (*Cooper*, 4547); Codakka (*C.* 4832); Singhi Djong (*C.* 4235); Cho La (*Ludlow and Sherriff*, 869); Me La (*L. and S.*, 889—form with monomorphic flowers); Chelai La, Ha (*L. and S.*, 3569).

TIBET: Sur La, Tsari (*Ludlow and Sherriff*, 2048); Kulu Phu Chu (*L., S. and Taylor*, 5975—form with monomorphic flowers); Mira La, Nyang Chu (*L., S. and T.*, 6125—form with monomorphic flowers); Di Chu Valley (*Ward*, 7175).

N.W. BURMA: Valley of the Seinghku (*Ward*, 7507).

P. capitata Hook. subsp. **lacteocapitata** (Balf. f. et W. W. Sm.)

W. W. Sm. et Forrest in *Notes Roy. Bot. Gard. Edin.*, xvi, 18 (1928), and in *Journ. Roy. Hort. Soc.*, liv, 35 (1929); Gould, *ibid.*, liv, 71 (1929); Bruun, *Cytological Studies in Primula*, 72, 127 (1932). *P. lacteocapitata* Balf. f. et W. W. Sm. in *Notes Roy. Bot. Gard. Edin.*, ix, 178, 185 (1916).

Very close to subsp. *Craibiana* with its narrow leaves and globose head. The leaves, however, are coated with cream-coloured farina on the lower surface, never with bright yellow farina as in subsp. *Craibiana*, and the leaf apex is far more pointed. From the rest of the section subsp. *lacteocapitata* may be distinguished by the bright-red bases of the petioles, but its divergence from the typical *P. capitata* is none too evident. It flowered in Edinburgh in 1916, but is now lost.

Represented in the Edinburgh Herbarium by the following:—

SIKKIM: Below Mome Samdong (*Cooper*, 428—*type*); Lachen (*C.* 438).

TIBET: Natu La to Champitang (*Spencer Chapman*, 406).

P. capitata Hook. subsp. **Mooreana** (Balf. f. et W. W. Sm.)

W. W. Sm. et Forrest in *Notes Roy. Bot. Gard. Edin.*, xvi, 18 (1928), and in *Journ. Roy. Hort. Soc.*, liv, 35 (1929); *ibid.*, liv, 35, 66, 71 (1929); Bruun, *Cytological Studies in Primula*,

72, 127 (1932). *P. Mooreana* Balf. f. et W. W. Sm. in Notes Roy. Bot. Gard. Edin., ix, 183 (1916); Besant in Irish Gardening, xiv, 63 (1919); Farrer in Engl. Rock Gard., ii, 117, 158 (1919); Gard. Chron., lxxii, 179, fig. 72 (1922); *ibid.*, lxxx, 87 (1926); The Garden, lxxxvi, fig. p. 465 (1922); *ibid.*, xc, 132, fig. p. 133 (1926); *ibid.*, xci, 581, with fig. (1927); Journ. Roy. Hort. Soc., xlviii, Proc. p. lxxxvi (1923); Cox and Taylor, Primulas, 94 (1928).

This plant is the most robust member of the aggregate and differs from typical *P. capitata* in the leaves being more rounded at the apex, efarinose above and up to 3 cm. in breadth, in the longer pedicels which may reach 6 mm., and in the more numerous and larger flowers with a very dense apical crown of imbricated bracts. It has been in culture for at least thirty years. The Hookerian type is in the Kew Herbarium and at Edinburgh are:—

SIKKIM: Lachen (*Native Collector* in 1922); Lachung (*Cave* in 1916).

P. capitata* Hook. subsp. *sphaerocephala (Balf. f. et Forrest) W. W. Sm. et Forrest in Notes Roy. Bot. Gard. Edin., xvi, 18 (1928), and in Journ. Roy. Hort. Soc., liv, 35 (1929); *ibid.*, liv, 61, 71, 79 (1929); Bruun, Cytological Studies in Primula, 72, 127 (1932). *P. sphaerocephala* Balf. f. et Forrest in Notes Roy. Bot. Gard. Edin., ix, 45 (1915); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 138, 154 (1913); Forrest, *ibid.*, xlii, 45 (1916). *P. pseudocapitata* Ward in Notes Roy. Bot. Gard. Edin., ix, 192 (1916); The Garden, lxxxvii, 124 (1923). *P. capitata* Forrest (nec Hook.) in Notes Roy. Bot. Gard. Edin., ix, 224 (1908).

The only member of the aggregate to extend into China. In its efarinose leaves it approaches closely to the Himalayan subsp. *crispata* from which it is difficult to discriminate it, but it has a somewhat different facies, less vigour, more funnel-shaped corolla, and a globular head of flowers. It was introduced to cultivation by Bees Ltd. in 1908 from Forrest's seed.

The plant is represented in the Edinburgh Herbarium by:—

YUNNAN: Kari Pass (*Forrest*, 46—*type*, 303); (*Ward*, 5317); Atuntze (*W.* 92A—*type* of *P. pseudocapitata*); Mountains N.E. of Atuntze (*F.* 20191); Legong, Mekong-Wi-chu divide (*W.* 5364); Bei-ma Shan, Mekong-Yangtze divide (*F.* 13215, 13432); Lukong Shan, Mekong-Yangtze divide (*F.* 14833); Likiang Snow Range (*Rock*, 24737); Mountains of Ludu, W. of the Yangtze (*R.* 18510).

S.E. TIBET: Tsarong, Ka-gwr-pu, Mekong-Salwin divide (*Forrest*, 14556, 15000); Salwin-Kiu-chiang divide (*F.* 19040); Temo La (*Ward*, 6184).

P. glomerata Pax in Engl. Pflanzenr. Primulaceae, 92 (1905); Craib in Journ. Roy. Hort. Soc., xxxix, 187 (1913); W. W. Sm. and *Forrest*, *ibid.*, liv, 34 (1929), and in Notes Roy. Bot. Gard. Edin., xvi, 21 (1928). *P. crispa* Balf. f. et W. W. Sm. in Notes Roy. Bot. Gard. Edin., ix, 160 (1916); Farrer, Engl. Rock Gard., ii, 117, 121 (1919); W. W. Sm. and *Forrest*, *ibid.*, xvi, 21 (1928), and in Journ. Roy. Hort. Soc., liv, 34 (1929); Adamson, *ibid.*, liv, 80 (1929); Bruun, Cytological Studies in Primula, 70, 127 (1932); Quart. Bull. Alp. Gard. Soc., ii, 26, fig. facing p. 29 (1933); W. W. Sm. in Proc. Linn. Soc., 170 (1933). *P. erosa* Hook. f. in Bot. Mag., t. 6916A (1887)—non Wall. *P. capitata* var. *crispa* Hort. *P. capitata* var. *erosa* Hort.

The type specimen of this species, *Scully* 287, is in the Breslau Herbarium and there are co-types at Kew, Calcutta, and Edinburgh. This Nepal material, collected about 1877, is of somewhat poor quality and does not give an adequate picture of the plant. Pax associated his species with *P. denticulata*, from which he discriminated it by the flowers being coetaneous with the distinctly petioled crose-denticulate leaves, by the absence of basal scales, and by the much shorter corolla-tube. The Tibetan example in the Berlin Herbarium (which one of us has seen), also quoted by Pax, corresponds with material under No. 451 in the Calcutta Herbarium obtained in 1882 at Khyelshima (*sic* ?) but without name of collector, and in any case imperfect. One result of this exiguous record was that *P. glomerata* was overlooked by Balfour (*l.c.*) in 1916 when he described *P. crispa* from Sikkim specimens. Nor was it evident to Smith and *Forrest* (*l.c.*) in 1928 that *P. crispa* is synonymous with *P. glomerata*. That this is the case was shown conclusively a few years later when copious material was secured from Nepal and the species again brought into cultivation. The first record of its flowering in culture would appear to be in 1887 when it was raised from Sikkim seed, figured in Botanical Magazine (*l.c.*) and wrongly identified with *P. erosa*. The figure was shown by Balfour (*l.c.*) to be a representation of his *P. crispa*. The species has a fairly wide distribution in Nepal and in Sikkim, and in that part of Tibet lying immediately north of Sikkim. The altitudinal range is very variously stated by collectors and on

their figures runs from 3300 m. to 5700 m. In Sikkim *P. glomerata* grows under the same conditions as *P. capitata*; in Nepal there is as yet no record of the occurrence of the latter.

The sectional position of *P. glomerata* is by no means certain. In the past it has been kept regularly in the same section as *P. denticulata*. The flowers of its dense capitulum are more or less erect and thus in line with the arrangement in section Denticulata, and not in accord with what is seen in *P. capitata*. But when the plant is examined in the living state and compared with living examples of the two allies quoted, then in its behaviour and in the general aspect of its foliage, inflorescence, and individual flower it favours Capitatae. On the other hand, the cytological data (Bruun, *l.c.*) support alignment with Denticulata. The plant requires further analysis, but we have no record of its survival in culture beyond 1939.

A sturdy plant with a short or long comparatively stout rhizome and devoid of bud-scales at the base but there sometimes clothed with the broad sheathing bases of old leaves. Leaves coactaneous with the flowers, including the petiole 3–15 cm. long, 1–3 cm. occasionally 4 cm. broad, oblong or oblanceolate or obovate-spathulate, rounded at the apex, attenuate into the winged petiole usually red at the base and shorter than the lamina but at times almost subequal, finely erose-denticulate at the margin, covered thinly above and thickly below with potentially farinose glands, often when young markedly white-farinose below; midrib broad and conspicuous; the numerous lateral nerves, and often the reticulation, prominent below. Scape 10–30 cm. tall, stout, erect, with farinipotent glands or even farina towards the apex, carrying a compact more or less globose head of flowers of which many stand erect; bracts numerous, clustered below the head and not forming an apical tuft, 6–12 mm. long, subfoliaceous, sometimes stained blackish-purple, narrowly ovate to lanceolate, glandular or farinose; pedicels almost obsolete or reaching 10 mm. long, farinose. Calyx 6–8 mm. long, tubular-campanulate, farinose within and without, cut to below the middle into lanceolate acute teeth. Corolla blue, infundibuliform, usually exannulate, sometimes annulate, heteromorphic, slightly farinose or conspicuously glandular within and without; tube only a little longer than the calyx or nearly twice as long; limb concave, 6–10 mm. in diameter with obcordate deeply emarginate lobes. Stamens, with anthers 2 mm. long, inserted two-thirds up corolla-tube or even higher in thrum-eyed flowers, near base of tube in pin-eyed. Long style reaching three-fourths

up corolla-tube; short style about 2 mm. long. Capsule ellipsoid, included in the calyx, dehiscing by longitudinal valves. Seeds similar to those of *P. capitata*.

The species is represented in the Edinburgh Herbarium by the following collections:—

NEPAL: (*Scully*, 287—*co-type*): Gossain Than (*Wall. Cat.* 607c); near Gossain Than (*Native Collector*, 124); Serkathan (*Sharma*, 396); Khimtee (*S.* 460); Feda (*S.* 506); Geyjung (*S.* 435); Paidung (*S.* 352, 353); Napchey (*S.* 354); Mulmulaykhola (*S.* 69); Jalpa (*Lal Dhwoj*, 315); sine loc. (*L. D.* 22, 40, 126).

SIKKIM: Ningbil (*Smith*, 4209—*type* of *P. crispa*); Lachung (*Gammie*, 799); Yampung (*Cave* in 1919); Tanka La (*Native Collector*); Peykiongla in 1888 (*King's Collector*); sine loc. (*Hooker*).

TIBET: West of Yatung (*Spencer Chapman*, 335); sine loc. (*Native Collector*, 451).

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KEYS TO THE SPECIES GROUPS OF QUERCUS, LITHOCARPUS, AND CASTANOPSIS OF EASTERN ASIA, WITH NOTES ON THEIR DISTRIBUTION. By E. C. BARNETT, D.Sc.

(Read 18th May 1944.)

Over 480 species of *Quercus*, *Lithocarpus*, and *Castanopsis* have been recorded from Asia, excluding species which are endemic to the Philippine Islands. Collectively, the three genera may be regarded as constituting the oaks of Asia, and while it is not possible at the present time to give a full account of all the species, an attempt is made in the following pages to arrange them in species groups. A tabular statement showing distribution of the species is also presented. For purposes of distribution Eastern Asia is divided into four main regions, and these in turn into smaller areas which are referred to in the tables by the abbreviations noted below.

1. *The Indo-Burmese region*, including the Indian Himalaya, Eastern Bengal and Assam (Ind.), Upper Burma (U.B.), and Thailand (Th.), excluding Peninsular Thailand.

2. *The Chinese region*, including China (Ch.), Hainan (Ha.), Korea (K.), Formosa (F.), and Japan (Jap.).

3. *The French Indo-Chinese region* (F.I.C.).

4. *The Malayan region*, including Lower Burma (L.B.), Peninsular Thailand (P.Th.), Malay Peninsula (M.P.), and Malay Islands (M.I.).

KEY TO THE GENERA.

- A. Stigmas covering the more or less recurved upper surface of the styles or capitate on them; male spikes pendulous, simple; stamens variable in number, most commonly six, anthers usually large; leaves usually serrate, dentate or lobed, seldom entire 1. *Quercus* Linn.
- AA. Stigma a terminal pore on the erect or slightly divergent styles; male spikes erect, simple or paniced; stamens usually twelve, anthers small, leaves entire or serrate or lobed.
 - B. Glans one per cupule; cupule cup-shaped or saucer-shaped or enclosing the glans, symmetrical, scales imbricate or lamellate, sometimes reduced to faint ridges; leaves entire, rarely serrate or lobed 2. *Lithocarpus* Blume
 - BB. Glans 1-4; cupules often oblique, enclosing the glans (except in some members of *C. fissa* group), often splitting irregularly, usually with spines or tubercles, occasionally with undulate ridges; leaves entire or serrate or lobed 3. *Castanopsis* Spach

THE GENUS QUERCUS LINN.

The genus may be divided into two sections:

Sect. LEPIDOBALANUS. Scales of the cupule imbricate p. 160

Sect. CYCLOBALANOPSIS. Scales of the cupule fused in entire or more or less denticulate lamellae p. 164

Sect. LEPIDOBALANUS.

This is a large section, most of the species being American. It is represented in Asia by 47 species which may be arranged in eight more or less distinct groups.

Key to Species Groups of Quercus, Sect. Lepidobalanus.

- A. Styles strap-like, revolute at the stigmatic tip.
 - B. Cupular scales adpressed; leaves small.
 - C. Lateral nerves slender, not conspicuously forked; glans ovoid.
 - 1. Group of *Q. ilex* Linn, p. 160
 - CC. Lateral nerves sturdy, distinctly forked; glans usually globose.
 - 2. Group of *Q. semecarpifolia* Smith, p. 161
 - BB. Cupular scales reflexed; leaves comparatively large.
 - 5. Group of *Q. serrata* Thunb., p. 162
 - AA. Styles strap-like, not revolute, whole upper surface stigmatic.
 - B. Leaves coarsely lobed or serrate, lower surface glabrous or pubescent.
 - C. Scales of the cupule short, more or less adpressed.
 - 6. Group of *Q. aliena* Blume, p. 162
 - CC. Scales of the cupule long, spreading.
 - 7. Group of *Q. dentata* Thunb., p. 163
 - BB. Leaves more or less sharply serrate, lower surface tomentose.
 - 8. Group of *Q. laevata* Smith, p. 163
 - AAA. Styles short, thick, stigmas widely revolute, subcapitate.
 - B. Leaves small.
 - 3. Group of *Q. Gilliana* Redh. and Wils., p. 161
 - BB. Leaves comparatively large.
 - 4. Group of *Q. Kingiana* Craib, p. 161

1. Group of *Q. ilex* Linn.

- 1. *Q. ilex* Linn.
- 2. *Q. acrodonta* Seem.
- 3. *Q. Handeliana* A. Cam.
- 4. *Q. phillyraeoides* Gray
- 5. *Q. setulosa* A. Cam.
- 6. *Q. singuliflora* A. Cam.
- 7. *Q. Wrightii* Nak.
- 8. *Q. dilatata* Lindl.

This group is distinctly northern with China as the chief centre. Although the type does not occur in China, it is widely distributed and is cultivated in many parts of Europe, including Great Britain. It is a native of Asia Minor where it is found in Lebanon at altitudes of from 1300–3000 m. It has been recorded from the Atlas Mountains of North Africa, and in India it extends from Afghanistan eastwards in the drier parts of the Himalaya as far as Simla, at elevations of 2000–3000 m. Four closely related species, *Q. acrodonta*, *Q. Handeliana*, *Q. phillyraeoides*, and *Q. singuliflora* are endemic to China. *Q. setulosa* occurs in Annam and Eastern Thailand, and *Q. Wrightii* is endemic to Japan.

The affinity of the Indian species, *Q. dilatata*, is difficult to de-

termine. It has affinity with *Q. ilex* and also with *Q. semecarpifolia* (Group 2). King describes it as "A gregarious evergreen tree, sometimes attaining a height of 80 feet. The leaves vary a good deal, those of the young shoots often having spiny edges. They are always glabrous when adult. The glabrescent forms of *Q. semecarpifolia* resemble this but are distinguished by their boldly bifurcating nerves and rather more rigid texture." In its ovoid glans it resembles *Q. ilex* and, although its leaves are usually larger than is typical for the group, its affinity seems to be with this group. In its thick stigmas it approaches the group of *Q. Gilliana*.

2. Group of *Q. semecarpifolia* Smith.

9. *Q. semecarpifolia* Smith
10. *Q. aquifolioides* Rehd. and Wils.
11. *Q. longispica* A. Cam.
12. *Q. pannosa* Hand.-Mazz.
13. *Q. pseudosemecarpifolia* A. Cam.
14. *Q. senescens* Hand.-Mazz.
15. *Q. spinosa* David

This group is also largely Chinese, all the species being found in China. The type species is widely distributed from Afghanistan and the North-West Provinces of India eastwards to Assam and S.E. Tibet, and occurs also in China and Thailand. One other species, *Q. senescens*, extends to India. With the exception of *Q. spinosa*, which occurs in Formosa, the others are endemic to China.

3. Group of *Q. Gilliana* Rehd. and Wils.

16. *Q. Gilliana* Rehd. and Wils.
17. *Q. cocciferoides* Hand.-Mazz.
18. *Q. laotica* A. Cam.
19. *Q. taliensis* A. Cam.
20. *Q. tarokoensis* Hay.

These species resemble those of groups 1 and 2 in leaf form, but differ in having the stigmas more or less capitate on the short styles, as in *Q. Kingiana*. *Q. laotica* is endemic to Laos; *Q. tarokoensis*, which is incompletely known, endemic to Formosa. The other three species are endemic to China.

4. Group of *Q. Kingiana* Craib.

21. *Q. Kingiana* Craib

This species has been recorded from Upper Burma and Thailand at altitudes of 1000–1600 m.

5. Group of *Q. serrata* Thunb.

- 22. *Q. serrata* Thunb.
- 23. *Q. Baronii* Skan
- 24. *Q. Chenii* Nakai
- 25. *Q. Moulei* Hance
- 26. *Q. spathulata* Seem.
- 27. *Q. variabilis* Blume

This group is essentially Chinese. With the exception of *Q. serrata* and *Q. variabilis* the species are endemic to China. *Q. serrata* is very widely distributed, being found in India as far west as Nepal and extending eastwards through Sikkim and Bhotan to Assam and Upper Burma. It is widely distributed in China and is found in Japan and Korea and as far south as Laos in French Indo-China. In Thailand it is restricted, so far as is at present known, to the eastern circle, Udawn, bordering Laos. *Q. serrata* is an ancient plant and probably had a wider distribution formerly. Seward, in his Presidential Address to the British Association in Dundee (1939), refers to fossil remains which closely resemble leaves of this species as having been found in Mull, where "pollen records show preponderance of eastern Asiatic species in the Hebridean flora." The species of this section of the genus (*Lepidobalanus*) are now largely American, but it seems probable that the section had a wider distribution formerly and that the Asiatic species represent a scattered remnant of a much more widely distributed group.

Q. variabilis is not found in India, but has been recorded from S.E. Tibet, China, Korea, and Formosa. It is found in Japan, but possibly only under cultivation.

6. Group of *Q. aliena* Blume.

- 28. *Q. aliena* Blume
- 29. *Q. Fabri* Hance
- 30. *Q. glandulifera* Blume
- 31. *Q. liaotungensis* Koidzumi
- 32. *Q. mongolica* Fischer

The following four Korean species (33-36) I have not seen, but the first three are given as having affinity with *Q. aliena*, the last as being a natural hybrid between *Q. serrata* and *Q. mongolica*, with leaves and branches like the former, cupule and nuts like the latter.

- 33. *Q. alienoides* Uyeki
- 34. *Q. paucilepis* Uyeki
- 35. *Q. pongtungensis* Uyeki
- 36. *Q. serratooides* Uyeki

The following two species form a connecting link between this group and the group of *Q. dentata*. In both the scales surrounding the mouth of the cupule are lengthened, those of *Q. Stewardii* being prolonged into bristles.

37. *Q. malacotricha* A. Cam.

38. *Q. Stewardii* Rehder

The chief centre of the *Q. aliena* group is China, where all the species are found with the exception of the four Korean species. The type species is widely distributed. It occurs in India from Sikkim to Assam, in Upper Burma, French Indo-China, Thailand, is common in China, and is found, rarely, in Japan. None of the other species is found in India. *Q. liaotungensis*, *Q. malacotricha*, and *Q. Stewardii* are endemic to China; *Q. Fabri* may also prove to be endemic, though it has been recorded, but with some degree of doubt, from Korea and Hainan. The other two species have been reported from Japan and Korea as well as China.

7. Group of *Q. dentata* Thunb.

39. *Q. dentata* Thunb.

40. *Q. augusta-lepidota* Nakai

41. *Q. pseudodentata* Uyeki

This group also belongs to the Chinese region. The type species occurs in China, Korea, Japan, and Formosa. The second species, which resembles the type very closely except that the cupular scales are thicker and shorter, has been recorded from Japan and Korea. The last species is endemic to Korea.

8. Group of *Q. lanata* Smith.

42. *Q. lanata* Smith

43. *Q. Franchetii* Skan

44. *Q. incana* Roxb.

45. *Q. lodicosa* Warburg

46. *Q. Engleriana* Seem.

Q. lanata and *Q. incana* are nearly related Himalayan species, and Smith, in his original description of *Q. lanata*, confused the two species. Typical specimens are quite distinct, but intermediate forms occur. *Q. incana* is commoner and has a wider distribution, extending from the North-West Provinces of India to Assam and Burma. *Q. lanata* does not occur farther west than Nepal and Kumaon. Both have been recorded from French Indo-China and Thailand, but it is possible that they have been confused with the

closely related *Q. Franchetii* which occurs in Thailand and Yunnan. *Q. lodicosa* is found in Burma and S.E. Tibet.

The affinity of *Q. Engleriana* has not been definitely established. It possibly belongs to this group, and Seemen, in his original description, gives it as having affinity with *Q. lanata*. It differs, however, in the styles being longer and in the stigmas being distinctly recurved. It does not have the characteristic, much-branched clothing hairs found in other members of the group. It is recorded from China and, doubtfully, from Upper Burma.

Species incompletely known.

47. *Q. dolichostyla* A. Cam.

This Chinese species is given by its author as incompletely known, but the suggestion is made that it may be related to *Q. Engleriana*.

Sect. CYCLOBALANOPSIS.

This section is entirely Asiatic. It is represented by 83 species forming seven more or less distinct groups.

Key to the Species Groups of Quercus, Sect. Cyclobalanopsis.

- A. Mature glans ovoid or globose-ovoid, longer than wide.
 - B. Styles long, stigmas wide recurved or capitate.
 - C. Cupule small, cup-shaped with numerous close lamellae.
 - D. Cupule glabrous or sparsely hairy.
 - 9. Group of *Q. glauca* Thunb., p. 164
 - DD. Cupule distinctly hairy both without and within.
 - 10. Group of *Q. acuta* Thunb., p. 165
 - CC. Cupule large, turbinate or cup-shaped, with distant lamellae, glabrous or tomentose without, usually densely silky within.
 - 11. Group of *Q. semiserrata* Roxb., p. 166
 - BB. Styles strap-like, whole upper surface stigmatic; cupule covering half or more of the glans.
 - 15. Group of *Q. oideocarpa* Korth, p. 168
- AA. Mature glans as wide or wider than long; styles short, stigmas wide or more or less capitate.
 - B. Glans hemispheric-conic, scar small.
 - 14. Group of *Q. Brandisiana* Kurz., p. 168
 - BB. Glans hemispheric or much flattened, scar large.
 - C. Leaves acuminate or caudate minutely or sharply serrate.
 - 12. Group of *Q. lineata* Blume, p. 167
 - CC. Leaves acute or obtuse, never caudate, coarsely serrate or serrate-lobed.
 - 13. Group of *Q. Helfferiana* A. DC., p. 168

9. Group of *Q. glauca* Thunb.

- 48. *Q. glauca* Thunb.
- 49. *Q. Augustinii* Skan
- 50. *Q. bambusifolia* Hance
- 51. *Q. Chevalieri* Hick. and A. Cam.
- 52. *Q. Delavayi* Franch.
- 53. *Q. djiringensis* A. Cam.

- 54. *Q. gilva* Blume
- 55. *Q. hunanensis* Hand.-Mazz.
- 56. *Q. myrsinaefolia* Blume
- 57. *Q. paucidentata* Franch. ex. Nak.
- 58. *Q. rupestris* Hick. and A. Cam.
- 59. *Q. salicina* Blume
- 60. *Q. saravanensis* A. Cam.
- 61. *Q. Sasakii* Kanehira
- 62. *Q. Schottkyana* Rehd. and Wils.
- 63. *Q. tranninhensis* Hick. and A. Cam.
- 64. *Q. xanthotricha* A. Cam.

The following species probably belong to this group:—

- 65. *Q. brevistyla* A. Cam.
- 66. *Q. Miyagii* Koid.
- 67. *Q. stenophylloides* Hayata
- 68. *Q. yayeyamensis* Koid.

This group is mainly Chinese. Only six of the twenty-one species do not occur in Chinese regions. Of these, five are endemic to French Indo-China, *Q. Chevalieri*, *Q. djiringensis*, *Q. rupestris*, *Q. saravanensis*, and *Q. xanthotricha*, while *Q. brevistyla* is endemic to the Malay Peninsula. The type species is widely distributed from the North-West Provinces of India eastwards to Assam, Upper Burma, S.E. Tibet, and China, Korea, Formosa, and Japan.

10. Group of *Q. acuta* Thunb.

- 69. *Q. acuta* Thunb.
- 70. *Q. Buergerii* Blume
- 71. *Q. Morii* Hayata
- 72. *Q. nubium* Hand.-Mazz.
- 73. *Q. sessilifolia* Blume

The following two species resemble those of this group but approach the group of *Q. semiserrata*, particularly in the somewhat longer styles and the fewer lateral nerves of the leaves:—

- 74. *Q. Championi* Benth.
- 75. *Q. Hui* Chun

Of the next species I have not seen a specimen, but it is given by its author as allied to *Q. Championi* Benth.

- 76. *Q. Chungii* Metcalf

The group of *Q. acuta* is restricted to Chinese regions. With the

exceptions of *Q. Buergerii*, endemic to Japan, and *Q. Morii*, endemic to Formosa, all the species occur in China. The type has the widest distribution, being found in China, Japan, and Korea.

11. Group of *Q. semiserrata* Roxb.

- 77. *Q. semiserrata* Roxb.
- 78. *Q. Blakei* Skan
- 79. *Q. cambodiensis* Hick. and A. Cam.
- 80. *Q. crassilamellata* A. Cam.
- 81. *Q. Edithae* Skan
- 82. *Q. Elmeri* Merr.
- 83. *Q. Fleuryi* Hick. and A. Cam.
- 84. *Q. glabricupula* Barnett
- 85. *Q. Horsfieldii* Miq.
- 86. *Q. lang-bianensis* Hick. and A. Cam.
- 87. *Q. longistyla* Barnett
- 88. *Q. pachyloma* Seem.
- 89. *Q. patkoiensis* A. Cam.
- 90. *Q. platycalyx* Hick. and A. Cam.
- 91. *Q. quangtriensis* Hick. and A. Cam.
- 92. *Q. Ramsbottomi* A. Cam.
- 93. *Q. tomentosicupula* Hayata
- 94. *Q. turbinata* Blume
- 95. *Q. wangsaiensis* Barnett
- 96. *Q. xanthoclada* Drake

It has not been possible to examine specimens of the following species (97-105), all of which are endemic to French Indo-China, with the exception of *Q. chrysocalyx* and *macrocalyx*, which also occur in Hainan, but from the descriptions it would appear that they belong to this group.

Q. Camusae differs from all other species of *Quercus* in having the cupules frequently fused in pairs.

- 97. *Q. asymmetrica* Hick. and A. Cam.
- 98. *Q. austrocochinchinensis* Hick. and A. Cam.
- 99. *Q. baniensis* A. Cam.
- 100. *Q. blaoensis* A. Cam.
- 101. *Q. Camusae* Trelease
- 102. *Q. chrysocalyx* Hick. and A. Cam.
- 103. *Q. donnaiensis* A. Cam.
- 104. *Q. macrocalyx* Hick. and A. Cam.
- 105. *Q. subumbilicata* A. Cam.

The distribution of the group is wider than that of any group dealt with so far. Representatives occur in all four regions. The largest number of species, seventeen, has been recorded from French Indo-China, fifteen being endemic. Five species, including three endemics, are found in Thailand. Five species occur in China. The group is represented in India by *Q. semisserata* and *Q. patkoiensis*, neither extending farther west than Assam. The type species is widely distributed in the Indo-Chinese Peninsula—in Upper and Lower Burma, Thailand, and French Indo-China, and has been recorded, although with some degree of doubt, from Malayan regions. Four species, *Q. crassilamellata*, *Q. turbinata*, *Q. Elmeri*, and *Q. Horsfieldii* are Malayan. The two former differ from the type in the ripe cupule retaining the juvenile turbinate form.

12. Group of *Q. lineata* Blume.

- 106. *Q. lineata* Blume
- 107. *Q. braianensis* A. Cam.
- 108. *Q. erioclada* A. Cam.
- 109. *Q. flavescens* Hick. and A. Cam.
- 110. *Q. fructiseptata* A. Cam.
- 111. *Q. lamellosa* Smith
- 112. *Q. oxyodon* Miq.
- 115. *Q. Rex* Hemsl.
- 114. *Q. vestita* Rehd. and Wils.

It has not been possible to examine material of the following three species, the first of which is endemic to Bengal, the others to French Indo-China, but they most probably belong to this group.

- 115. *Q. Gambleana* A. Cam.
- 116. *Q. chapensis* Hick. and A. Cam.
- 117. *Q. Dussaudii* Hick. and A. Cam.

The group is widely distributed and is represented in all four regions. There are two main centres of distribution, the Indo-Burmese region and French Indo-China. The type species, of which there are several well-marked varieties, is found in the Himalaya from Sikkim eastwards and occurs in Assam, Upper and Lower Burma, Thailand, and has also been recorded from Java. Five species are Indo-Burmese, *Q. Gambleana*, *Q. lamellosa*, *Q. oxyodon*, *Q. Rex*, and *Q. vestita*, the last extending through the Indo-Chinese Peninsula to Lower Burma. Eight species, five of which are endemic, are found in French Indo-China. The group is

represented in China by *Q. oxyodon* and *Q. Rex*, and in Hainan by *Q. flavescens*.

13. Group of *Q. Helferiana* A. DC.

- 118. *Q. Helferiana* A. DC.
- 119. *Q. dilacerata* Hick. and A. Cam.
- 120. *Q. Kerrii* Craib
- 121. *Q. mespilifolia* Wall.
- 122. *Q. Thorelii* Hick. and A. Cam.

This group is essentially Indo-Chinese. The type species and *Q. mespilifolia* are found as far west as Assam and Eastern Bengal. None of the other species occurs in India. All are found in French Indo-China, *Q. dilacerata* and *Q. Thorelii* being endemic. The group is represented in Thailand by *Q. Helferiana* and *Q. Kerrii*, the former extends southwards to Lower Burma and is the only representative in China. A narrow-leaved variety of *Q. Kerrii* occurs in Peninsular Thailand.

14. Group of *Q. Brandisiana* Kurz.

- 123. *Q. Brandisiana* Kurz

This distinctive species occurs in Upper Burma and in N.W. Thailand at altitudes of from 500–1500 m.

15. Group of *Q. oidocarpa* Korth.

- 124. *Q. oidocarpa* Korth
- 125. *Q. argentata* Korth
- 126. *Q. Hendersoniana* A. Cam.
- 127. *Q. Jenseniana* Hand.-Mazz.
- 128. *Q. lenticellata* Barnett
- 129. *Q. Lowii* King
- 130. *Q. nivea* King

This is essentially a Malayan group. The type species occurs in Sumatra, Borneo, the Malay Peninsula, and extends as far north as Lower Burma and Peninsular Thailand. With the exceptions of *Q. Jenseniana* and *Q. lenticellata*, endemic to China and Thailand respectively, the others are purely Malayan.

The position of the following species (131–143) is doubtful. Many of them have been described by their authors from immature material.

- 131. *Q. arbutifolia* Hick. and A. Cam. French Indo-China
- 132. *Q. argyrotricha* A. Cam., possibly *Q. lineata* Group. China

- 133. *Q. auricoma* A. Cam. China
- 134. *Q. caudatilimba* Merr. China and Hainan
- 135. *Q. doichangensis* A. Cam. Thailand
- 136. *Q. eumorpha* Kurz, possibly *Q. glauca* Group. Upper Burma
- 137. *Q. Hondai* Makino. Japan
- 138. *Q. hypophaea* Hay. Formosa
- 139. *Q. kontumensis* A. Cam. given as very different from all known species—with entire leaves. French Indo-China
- 140. *Q. litseoides* Dunn. China
- 141. *Q. Poilanei* Hick. and A. Cam. French Indo-China and China
- 142. *Q. Stewardiana* A. Cam., possibly near *Q. dilacerata* of the *Q. Helferiana* Group. China
- 143. *Q. Treubiana* Seem., possibly *Q. semiserrata* Group. Borneo

The following two Korean species I have not seen nor have I been able to consult the literature.

- 144. *Q. crispuloides* Uyeki
- 145. *Q. neo-glandulosa* Uyeki

THE GENUS LITHOCARPUS BLUME.

The genus is entirely Asiatic. It may be divided into five sections as follows:—

- A. Cupule not longer than the glans.
- B. Cupule scutelliform, saucer or cup-shaped.
 - C. Cupular scales distinct, imbricate or more or less arranged in rings but not fused to form lamellae Sect. PASANIA, p. 169
- CC. Cupular scales fused to form entire or denticulate lamellae.
 - Sect. CYCLOBALANUS, p. 176
- BB. Cupule covering the glans completely except for the umbo and styles.
 - C. Cupule not fused with the glans except at the base.
 - Sect. CHLAMYDOBALANUS, p. 178
- CC. Cupule more or less completely fused with the glans.
 - Sect. SYNAEDRYS, p. 179
- AA. Cupule distinctly longer than the glans Sect. CORYLOPASANIA, p. 181

Sect. PASANIA.

This is the largest section of the genus, comprising almost fifty per cent. of the total number of species. It may be divided into twelve more or less distinct species groups.

Key to Species Groups of *Lithocarpus*, Sect. *Pasania*.

A. Cupular scales long recurved.

B. Cupule saucer-shaped, covering the base of the glans only.

1. Group of *L. Scortechinii* (King) A. Cam., p. 170

BB. Cupule cup-shaped or more or less globose, covering more than half or almost completely, the glans.

2. Group of *L. lappaceus* (Roxb.) Rehd., p. 171

AA. Cupular scales short.

B. Cupular scales adpressed but with the acute or acuminate tips free, often reflexed, occasionally incurved at mouth, always distinct.

C. Cupule saucer-shaped or scutelliform; glans hemispheric-conic or ovoid-conic.

3. Group of *L. sundaicus* (Blume) Rehd., p. 171

CC. Cupule sub-globose covering more than half of the glans, often covering it completely except for the umbo and styles.

4. Group of *L. fenestratus* (Roxb.) Rehd., p. 172

BB. Cupular scales adpressed, tips sometimes free but never reflexed.

C. Glans ovoid or cylindric-conic, distinctly longer than wide.

D. Cupule cup-shaped or saucer-shaped.

E. Cupule small, up to 1.5 cm. diameter, glabrous.

5. Group of *L. glaber* (Thunb.) Nak., p. 173

EE. Cupule over 1.5 cm. wide, sometimes large, mouth may be recurved.

F. Cupule velvety without; leaves tawny pubescent below or with the veins tawny pubescent.

6. Group of *L. Kunstleri* (King) A. Cam., p. 174

FF. Ripe cupule more or less glabrous without, not velvety, may be velvety within; leaves usually glabrous, may be puberulous or granular but not pubescent.

7. Group of *L. Falconeri* (Kurz) Rehd., p. 174

DD. Cupule scutelliform, covering the base only of the glans.

8. Group of *L. Curtisii* (King) A. Cam., p. 174

CC. Glans ovoid-conic to depressed-globose, not distinctly longer than broad.

D. Cupular scales usually thickened, often umbonate, glans glabrous, fruits usually crowded on the rachis.

9. Group of *L. spicatus* (Smith) Rehd., p. 174

DD. Cupular scales not thickened, arranged more or less distinctly in rings.

E. Cupules sessile, glans pubescent.

10. Group of *L. Thomsoni* (Miq.) Rehd., p. 175

EE. Cupules pedicellate, glans glabrous.

11. Group of *L. polystachyus* (Wall.) Rehd., p. 176

CCC. Glans hemispheric more or less flattened, distinctly wider than high.

12. Group of *L. pallidus* (Blume) Rehd., p. 176

1. Group of *L. Scortechinii* (King) A. Cam.

1. *L. Scortechinii* (King) A. Cam.

2. *L. Arecus* (Hick. and A. Cam.) A. Cam.

3. *L. cyrtocarpus* (Drake) A. Cam.

This group is absent from the Indo-Burmese and Chinese regions. The type species occurs in the Malay Peninsula and in Peninsular Thailand. The other two species are endemic to Tonkin in French Indo-China.

2. Group of *L. lappaceus* (Roxb.) Rehd.

4. *L. lappaceus* (Roxb.) Rehd.
5. *L. Bonnetii* (Hick. and A. Cam.) A. Cam.
6. *L. echinocarpus* (Hick. and A. Cam.) A. Cam.
7. *L. echinophorus* (Hick. and A. Cam.) A. Cam.
8. *L. Garrettianus* (Craib) A. Cam.
9. *L. hypophoeniceus* (Seem.) Barnett
10. *L. Kingianus* (Gamble) A. Cam.
11. *L. longispinus* Barnett
12. *L. recurvatus* Barnett
13. *L. reflexus* (King) A. Cam.
14. *L. Rodgerianus* A. Cam.
15. *L. Skanianus* (Dunn) Rehd.
16. *L. Wrayii* (King) A. Cam.

The last species will, it seems probable, be reduced to *L. lappaceus* when more material is available, the type specimen in the Herbarium at Kew having fruit which is not quite mature. I can find no difference between it and *L. lappaceus*.

This group is widely distributed, the type species, *L. lappaceus*, occurring in India, in Eastern Bengal and Assam, Upper Burma, Thailand, in circles of Northern, Southern, and Peninsular regions, and in the Malay Peninsula. Four species are endemic to Malayan areas, two to Thailand, one to Lower Burma, three to French Indo-China; one species is found both in Thailand and French Indo-China. *L. Skanianus* occurs in China and Hainan. The distribution of the group as a whole thus resembles that of the type species.

3. Group of *L. sundaicus* (Blume) Rehd.

17. *L. sundaicus* (Blume) Rehd.
18. *L. celebicus* (Miq.) Rehd.
19. *L. conocarpus* (Oudem.) Rehd.
20. *L. dasystachyus* (Miq.) Rehd.
21. *L. hystrix* (Korth) Rehd.
22. *L. lampongus* (Miq.) Rehd.
23. *L. Winklerianus* (Schky.) A. Cam.

The following three species resemble those of this group in fruit, but in leaf form they resemble more closely those of the *L. Falconeri* group. The fruits of *L. elephantum* have the cupular scales somewhat lamellate, thus resembling those of sect. 2, *Cyclobalanus*.

- 24. *L. grandifrons* (King) A. Cam.
- 25. *L. gigantophyllus* (Hick. and A. Cam.) A. Cam.
- 26. *L. elephantum* (Hance) A. Cam.

I have not seen specimens of the following two species, but they are given by their authors as being near *L. sundaicus*; *L. pseudosundaicus* is also given as approaching *L. spicatus* (Group 9).

- 27. *L. pseudosundaicus* (Hick. and A. Cam.) A. Cam.
- 28. *L. Finetii* (Hick. and A. Cam.) A. Cam.

This group is typically Malayan. With the exceptions of *L. gigantophyllus*, *L. elephantum*, *L. pseudosundaicus*, and *L. Finetii*, all of which are endemic to French Indo-China, the species are Malayan. The type species extends northwards into Peninsular Thailand.

4. Group of *L. fenestratus* (Roxb.) Rehd.

- 29. *L. fenestratus* (Roxb.) Rehd.
- 30. *L. acuminatus* (Roxb.) Rehd.
- 31. *L. Cottonii* A. Cam.
- 32. *L. Craibianus* Barnett
- 33. *L. dealbatus* (Hook. f. and Th.) Rehd.
- 34. *L. elaeagnifolius* (Seem.) Chun
- 35. *L. Elizabethae* (Tutch.) Rehd.
- 36. *L. Handelianus* A. Cam.
- 37. *L. kemmaratensis* (Hick. and A. Cam.) A. Cam.
- 38. *L. pycnostachyus* A. Cam.
- 39. *L. rhabdostachyus* (Hick. and A. Cam.) A. Cam.
- 40. *L. tephrocarpus* (Drake) A. Cam.
- 41. *L. triqueter* (Hick. and A. Cam.) A. Cam.

The following three species have affinity with this group and also with the group of *L. spicatus*. They differ from *L. fenestratus* in the cupule covering not more than half to two-thirds of the glans and from *L. spicatus* in the cupular scales not being thickened and umbonate.

- 42. *L. intermedius* Barnett
- 43. *L. braianensis* A. Cam.
- 44. *L. synbalanos* (Hance) Chun

The following species I have not seen, but it is given by its author as having affinity with *L. fenestratus* and *L. spicatus* and also recalling *L. truncatus* (Group 20, *Synaedrys* sect.).

- 45. *L. variolosus* (Franch.) Chun

The group of *L. fenestratus* is an interesting one, some of the species apparently forming a connecting link between the *Pasania* and *Synaedrys* sections. Most commonly the scar of the glans is small and basal, but in *L. Elizabethae*, *L. Craibianus*, and *L. pyenostachyus* the scar is much larger, occupying half or more of the glans, thus approaching *L. truncatus* of the *Synaedrys* section. The glans is, however, quite free from the cupule, not fused with it as it is in that section. *L. Craibianus* and *L. pyenostachyus* also resemble *L. truncatus* in having the cupular wall thicker than is usual in this group and in having the scales somewhat incurved round the mouth.

The group is essentially northern, although *L. intermedius* and possibly *L. fenestratus* are found in Peninsular Thailand. An Indo-Burmese element comprises six species, two of which, *L. fenestratus* and *L. dealbatus*, extend eastwards to China and French Indo-China. There is a large French Indo-Chinese element of eight, possibly nine, species, six of which are endemic. China has three and Hainan two endemic species.

5. Group of *L. glaber* (Thunb.) Nak.

46. *L. glaber* (Thunb.) Nak.
47. *L. brunneus* Rehd.
48. *L. dodonaeifolius* (Hay.) Hay.
49. *L. edulis* (Mak.) Nak.
50. *L. elatus* (Hick. and A. Cam.) A. Cam.
51. *L. eucalyptifolius* (Hick. and A. Cam.) A. Cam.
52. *L. formosanus* (Skan) Rehd.
53. *L. Hancei* (Benth.) Rehd.
54. *L. Harlandii* (Hance) Rehd.
55. *L. Irwinii* (Hance) Rehd.
56. *L. iteaphyllus* (Hance) Rehd.
57. *L. Krempfii* (Hick. and A. Cam.) A. Cam.
58. *L. Mairei* (Schky.) Rehd.
59. *L. naiadarum* (Hance) Chun
60. *L. silvicularum* (Hance) Chun
61. *L. taitoensis* (Hay.) Hay.
62. *L. ternaticupulus* (Hay.) Hay.
63. *L. viridis* (Schky.) Rehd. and Wils. This species has affinity also with *L. polystachyus* (Group 11), but differs from the latter in having sessile cupules.

The group is essentially Chinese. Of the eighteen species, fifteen occur in this region, six being endemic to China. Three

species are endemic to French Indo-China. The group is represented in the Indo-Burmese region by one Chinese species, *L. viridis*, which occurs in Upper Burma.

6. Group of *L. Kunstleri* (King) A. Cam.

64. *L. Kunstleri* (King) A. Cam.

The following two species have affinity with *L. Kunstleri* and also with the *L. Falconeri* group.

65. *L. ochraceus* (Schky.) A. Cam.

66. *L. borneensis* (Merr.) Rehd.

This is a Malayan group. The type species occurs in the Malay Islands and in the Peninsula and extends northwards into French Indo-China. The other two are endemic to Borneo.

7. Group of *L. Falconeri* (Kurz) Rehd.

67. *L. Falconeri* (Kurz) Rehd.

68. *L. Amherstianus* (Wall.) A. Cam.

69. *L. bancanus* (Scheff.) Rehd.

70. *L. craterophorus* (Fisch.) A. Cam.

71. *L. rufescens* Barnett

72. *L. scyphiger* (Hance) A. Cam.

This group is also Malayan. The type has the widest distribution, occurring in the Malay Peninsula, Lower Burma, and Peninsular Thailand. *L. Amherstianus* occurs farthest north, being endemic to the Amherst region of Burma. *L. bancanus* and *L. scyphiger* occur only in the Malay Islands.

8. Group of *L. Curtisii* (King) A. Cam.

73. *L. Curtisii* (King) A. Cam.

74. *L. cerifer* (Hick. and A. Cam.) A. Cam.

The type species is Malayan but extends northwards to Peninsular Thailand. The other is endemic to French Indo-China, occurring in Cambodia and CochinChina.

9. Group of *L. spicatus* (Smith) Rehd. and Wils.

75. *L. spicatus* (Smith) Rehd. and Wils.

76. *L. annamensis* (Hick. and A. Cam.) Barnett

77. *L. bacgiangensis* (Hick. and A. Cam.) A. Cam.

78. *L. brevicaudatus* (Skan) Rehd.

79. *L. chittagongus* (Hick. and A. Cam.) Barnett

80. *L. Ducampii* (Hick. and A. Cam.) A. Cam.

81. *L. Henryi* (Seem.) Rehd. and Wils.
82. *L. Kawakamii* (Hay.) Hay.
83. *L. megalophyllus* Rehd. and Wils.
84. *L. Pierrei* (Hick. and A. Cam.) A. Cam.
85. *L. sabulicolus* (Hick. and A. Cam.) A. Cam.
86. *L. seishoi* (Hay.) Barnett
87. *L. erythrocarpus* (Ridl.) A. Cam.

I have not seen specimens of the following species, all of which are endemic to French Indo-China, but by the descriptions they appear to be near this group.

88. *L. auriculatus* (Hick. and A. Cam) Barnett
89. *L. bassacensis* (Hick. and A. Cam.) Barnett
90. *L. parvulus* (Hick. and A. Cam.) A. Cam.

Sub-group of *L. Lindleyanus* (Wall.).

The following two species are nearly related to *L. spicatus*, but they differ in the cupules being smaller, the glans ovoid-conic, never depressed. The cupules have the umbonate scales of the *spicatus* type.

91. *L. Lindleyanus* (Wall.) A. Cam.
92. *L. Harmandii* (Hick. and A. Cam.) A. Cam.

L. spicatus is very widely distributed and, as might be expected, is variable. It occurs in the Indian Himalaya and extends eastwards to S.E. Tibet and China, and southwards through the Indo-Chinese Peninsula to Malaya, where it occurs in both the Peninsula and the Islands. One other species, *L. erythrocarpus*, which is not altogether typical of the group, occurs in the Malay Peninsula, where it is endemic. Apart from the type, only *L. chittagongus* is recorded from India and is restricted to Assam. Of the others eight are endemic to French Indo-China, while seven occur in Chinese areas; the two species of the sub-group are restricted to the Indo-Chinese Peninsula.

10. Group of *L. Thomsoni* (Miq.) Rehd.

93. *L. Thomsoni* (Miq.) Rehd.
94. *L. litseifolius* (Hance) Chun
95. *L. mucronatus* (Hick. and A. Cam.) A. Cam.
96. *L. vestitus* (Hick. and A. Cam.) A. Cam.
97. *L. Wallichianus* (Lindl.) Rehd.

The type species is widely distributed from the Eastern Himalaya through Assam and Burma to Thailand and Indo-China. *L.*

Wallichianus has a much more restricted distribution in the Malay Peninsula, extending northwards into Peninsular Thailand. Two species, *L. litseifolius* and *L. vestitus*, belong to the Chinese region. *L. mucronatus* is endemic to French Indo-China.

11. Group of *L. polystachyus* (Wall.) Rehd.

98. *L. polystachyus* (Wall.) Rehd.

99. *L. farinulenta* (Hance) A. Cam.

This is a group of the Indo-Chinese Peninsula. The type occurs in Upper and Lower Burma and Thailand, the other is endemic to French Indo-China.

12. Group of *L. pallidus* (Blume) Rehd.

100. *L. pallidus* (Blume) Rehd.

101. *L. Carolinae* (Skan) Rehd.

102. *L. crassinervius* (Blume) Rehd.

103. *L. daphnoideus* (Blume) A. Cam.

104. *L. dolichocarpus* (Seem.) Rehd.

105. *L. Havilandii* (Stapf) Barnett

106. *L. monticolus* (King) Rehd.

107. *L. pruinosis* (Blume) Rehd.

108. *L. pseudo-moluccus* (Blume) Rehd.

With but one exception, *L. Carolinae*, endemic to China, the species of this group are found in the Malay Islands. *L. pallidus* and *L. Havilandii* are also found in the Philippines.

Sect. CYCLOBALANUS.

This section of the genus is almost entirely Malayan. It may be divided into three more or less distinct groups.

Key to Species Groups of Lithocarpus, Sect. Cyclobalanus.

A. Cupules pedicellate.

B. Pedicels distinct, glans hemispheric-apiculate to hemispheric-depressed . 13. Group of *L. Reinwardtii* (Korth) A. Cam., p. 176

BB. Pedicels very short, cupule tapering to a stalk-like base, glans ovoid-conic or depressed globose or turbinate.

14. Group of *L. cyrtorhynchus* (Miq.) Rehd., p. 177

AA. Cupules sessile, glans much wider than long c. 2-4 cm. diameter.

15. Group of *L. omalokos* (Korth) Rehd., p. 177

13. Group of *L. Reinwardtii* (Korth) A. Cam.

109. *L. Reinwardtii* (Korth) A. Cam.

110. *L. Cantleyanus* (King) Rehd.

111. *L. longipedicellatus* (Hick. and A. Cam.) A. Cam.

- 112. *L. magneinii* (Hick. and A. Cam.) A. Cam.
- 113. *L. poculiformis* (Seem.) A. Cam.
- 114. *L. sootepensis* (Craib) A. Cam.
- 115. *L. tenuinervis* (Hick. and A. Cam.) A. Cam.

This is a group of Malayan regions and the Indo-Chinese Peninsula. The type species occurs in Sumatra and French Indo-China and has been recorded, with some degree of doubt, from Peninsular and Southern Thailand. The other Malayan species are *L. Cantleyanus* from the Malay Peninsula, extending northwards into Lower Burma and Thailand, and *L. poculiformis*, endemic to Borneo. The other species are Indo-Chinese. *L. magneinii* has also been recorded from India, but no locality is mentioned. *L. sootepensis* is endemic to Thailand, the remaining two species to French Indo-China.

14. Group of *L. cyrtorhynchus* (Miq.) Rehd.

- 116. *L. cyrtorhynchus* (Miq.) Rehd.
- 117. *L. Bennettii* (Miq.) Rehd.
- 118. *L. clathratus* (Seem.) Rehd.
- 119. *L. Clementianus* (King) A. Cam.
- 120. *L. Eichleri* (Wenzig) A. Cam.
- 121. *L. Ewyckii* (Korth) Rehd.
- 122. *L. heliciformis* (Seem.) Rehd.
- 123. *L. Rangerianus* A. Cam.
- 124. *L. rassus* (Miq.) Rehd.
- 125. *L. Ridleyanus* A. Cam.
- 126. *L. Symingtonianus* A. Cam.
- 127. *L. Wenzigianus* (King) A. Cam.

These species are all Malayan. *L. Eichleri* and *L. Clementianus* possibly extend northwards into Thailand, but as the available Thai material is immature they have been identified with some degree of doubt.

15. Group of *L. omalokos* (Korth) Rehd.

- 128. *L. omalokos* (Korth) Rehd.
- 129. *L. costatus* (Blume) Rehd.
- 130. *L. cyclophorus* (Endl.) A. Cam.
- 131. *L. Diepenhorstii* (Miq.) Barnett
- 132. *L. Dunnii* Metcalf
- 133. *L. lampadarius* (Gamble) A. Cam.

- 134. *L. lucidus* (Roxb.) Rehd.
- 135. *L. platycarpus* (Blume) Rehd.
- 136. *L. rajah* (Hance) A. Cam.
- 137. *L. Teysmannii* (Blume) Rehd.

This also is a typically Malayan group, with the exception of *L. Dunnii*, which is endemic to China. The type species and *L. cyclophorus* extend northwards from the Malay Islands and Peninsula into Peninsular Thailand. The type also occurs in Lower Burma.

Sect. CHLAMYDOBALANUS.

This is a small section the species of which may be referred to a single group.

- 16. Group of *L. encleisacarpus* (Korth) A. Cam.
 - 138. *L. encleisacarpus* (Korth) A. Cam.
 - 139. *L. aggregatus* Barnett
 - 140. *L. attenuatus* (Skan) Rehd.
 - 141. *L. Blumeanus* (Korth) Rehd.
 - 142. *L. confragosus* (King) A. Cam.
 - 143. *L. echinifer* (Merr.) A. Cam.
 - 144. *L. Macphailii* (Henderson) Barnett
 - 145. *L. pattaniensis* Barnett
 - 146. *L. Robinsonii* (Ridley) Rehd.
 - 147. *L. stenopus* (Hick. and A. Cam.) A. Cam.
 - 148. *L. indutus* (Blume) Rehd.

The following five French Indo-Chinese species (149–153) possibly belong to this group, but I have seen no material in fruit.

- 149. *L. coinhensis* (Hick. and A. Cam.) A. Cam.
- 150. *L. Paviei* (Hick. and A. Cam.) A. Cam.
- 151. *L. Rouletii* (Hick. and A. Cam.) A. Cam.
- 152. *L. sphaerocarpus* (Hick. and A. Cam.) A. Cam.
- 153. *L. trachycarpus* (Hick. and A. Cam.) A. Cam.

There would appear to be two main centres of distribution in this group, Malaya and Indo-China. The five species of doubtful affinity and *L. stenopus* are endemic to French Indo-China. *L. aggregatus* and *L. pattaniensis* are endemic to Thailand, the former occurring in the N.W. and the latter in the Peninsular area. *L. attenuatus* is endemic to China. All the others are confined to Malayan areas.

Sect. SYNAEDRYS.

Key to Species Groups of *Lithocarpus*, Sect. *Synaedrys*.

A. Cupules symmetrical.

B. Cupular scales thick, somewhat reflexed or tuberculate.

17. Group of *L. xylocarpus* (Kurz) Markgraf, p. 179

BB. Cupular scales distinct, imbricate, but not reflexed.

18. Group of *L. corneus* (Lour.) Rehd., p. 179

BBB. Cupular scales more or less indistinct, arranged in rings.

19. Group of *L. truncatus* (King) Rehd. and Wils. p. 180

AA. Cupules asymmetrical, bearing zones or rings, but not scales.

20. Group of *L. javensis* Blume, p. 18017. Group of *L. xylocarpus* (Kurz) Markgraf.154. *L. xylocarpus* (Kurz) Markgraf.155. *L. annamitorum* (Cheval) A. Cam.156. *L. Milroyi* (Purk.) Barnett157. *L. Parkinsonii* A. Cam.158. *L. Rosthornii* (Schky.) Barnett

This group has a comparatively restricted distribution in northern areas from Assam to Indo-China and China. All are endemic species. *L. xylocarpus* and *L. Milroyi* to Assam, *L. Parkinsonii* to Upper Burma, *L. annamitorum* to French Indo-China, and *L. Rosthornii* to China.

18. Group of *L. corneus* (Lour.) Rehd.159. *L. corneus* (Lour.) Rehd.160. *L. comptus* (Seem.) Barnett161. *L. Fordianus* (Hemsl.) Chun162. *L. hemisphaericus* (Drake) Barnett163. *L. lycorperdon* (Skan) A. Cam.164. *L. magnificus* (Brandis) A. Cam.165. *L. pachyphyllus* (Kurz) Rehd.166. *L. pulcher* (King) Markgraf.167. *L. rotundatus* (Blume) A. Cam.168. *L. uvariifolius* (Hance) Rehd.

I have not seen the following species. It is given by its author as having fruit like that of *L. corneus*, but differing in the cupule and as having slight resemblance to *L. magnificus* and *L. platycarpus* of the *L. omalokos* group.

169. *L. pseudoplatycarpus* A. Cam.

Most of the *L. corneus* group are species of the northern regions, China and French Indo-China being the chief centres. The type species is widely distributed, occurring in French Indo-China,

Hainan, and the Malay Islands. Three species, *L. pseudoplatycarpus*, *L. rotundifolius*, and *L. pulcher* are Malayan, the first endemic to the Peninsula, the others to Java and Borneo respectively. Two species belong to the Indo-Burmese flora, *L. pachycarpus*, with a comparatively wide distribution from the Himalaya of Sikkim to Burma, and *L. magnificus* an endemic of Upper Burma. The other five species occur in China or French Indo-China, or both.

19. Group of *L. truncatus* (King) Rehd. and Wils.

- 170. *L. truncatus* (King) Rehd. and Wils.
- 171. *L. amygdalifolius* (Skan) Hay.
- 172. *L. Balansae* (Drake) A. Cam.
- 173. *L. baviensis* (Drake) A. Cam.
- 174. *L. castanopsisifolius* (Hay.) Hay.
- 175. *L. cleistocarpus* (Seem.) Rehd. and Wils.
- 176. *L. laoticus* (Hick. and A. Cam.) A. Cam.
- 177. *L. megastachyus* (Hick. and A. Cam.) A. Cam.
- 178. *L. Ollus* (Kurz) A. Cam.
- 179. *L. pachycarpus* (Hick. and A. Cam.) A. Cam.

The following species, endemic to the Malay Peninsula, I have not seen, but it is given by its author as having affinity with *L. laoticus*.

- 180. *L. Hendersonianus* A. Cam.

With the exception of the last species this is a northern group, with French Indo-China as the main centre. Six species, five of which are endemic, are found there. The type species is comparatively widely distributed from E. Bengal and Assam eastwards to Burma, Thailand, and French Indo-China. It is not found in China but is replaced there by *L. cleistocarpus*, a very closely related species which may be merely a form of *truncatus*. *L. amygdalifolius* occurs in China, Hainan, and Formosa. *L. castanopsisifolius* is endemic to Formosa, *L. Ollus* to Assam.

20. Group of *L. javensis* Blume.

- 181. *L. javensis* Blume
- 182. *L. Beccarianus* (Benth.) A. Cam.
- 183. *L. Burkilli* A. Cam.
- 184. *L. Maingayi* (Benth.) Rehd.
- 185. *L. scutigera* (Oude.) A. Cam.
- 186. *L. subnuciferus* A. Cam.
- 187. *L. pyriformis* (Seem.) Rehd.

This group is entirely Malayan. *L. Beccarianus* occurs in both the Peninsula and the islands. *L. Burkilli*, *L. Maingayi*, and *L. subnuciferus* are endemic to the Peninsula. The others are restricted to the islands.

Sect. CORYLOPASANIA.

21. Group of *L. nhatrangensis* (Hick. and A. Cam.) A. Cam.

188. *L. nhatrangensis* (Hick. and A. Cam.) A. Cam.

189. *L. proboscidius* (Hick. and A. Cam.) A. Cam.

190. *L. tubulosus* (Hick. and A. Cam.) A. Cam.

The three species of this small group are known only from French Indo-China.

The following species I have not seen and in some cases have not been able to consult the literature. As it has not been possible to place them in their groups, they are listed here according to their geographical distribution.

CHINESE REGION.

Formosa.

191. *L. arisanensis* (Hay.) Hay.

192. *L. hypophaeus* (Hay.) Hay.

193. *L. impressivenus* (Hay.) Hay.

194. *L. kodaihoensis* (Hay.) Hay.

195. *L. Konishii* (Hay.) Hay.

196. *L. lepidocarpus* (Hay.) Hay.

197. *L. longicaudatus* (Hay.) Hay.

198. *L. nantoensis* (Hay.) Hay.

199. *L. randaiensis* (Hay.) Hay.

200. *L. rhombocarpus* (Hay.) Hay.

201. *L. subreticulatus* (Hay.) Hay.

202. *L. suishaensis* Kanehira and Yamamoto

203. *L. uraianus* (Hay.) Hay.

Hainan.

204. *L. Fenzelianus* A. Cam.

FRENCH INDO-CHINA.

205. *L. cambodiensis* A. Cam.

206. *L. cryptocarpus* A. Cam.

207. *L. gymnocarpus* A. Cam.

208. *L. honbaensis* A. Cam.

209. *L. leiostachyus* A. Cam.

210. *L. leucostachyus* A. Cam.

211. *L. micropermus* A. Cam.

212. *L. nebularum* A. Cam.

213. *L. Petelotii* A. Cam.

214. *L. platyphyllus* A. Cam.

215. *L. pleiocarpus* A. Cam.

216. *L. Yersinii* A. Cam.

The following are stated by their authors as incompletely known. Most have been described from immature material.

217. *L. coalitus* (Hick. and A. Cam.) A. Cam., possibly near *L. spicatus*.

218. *L. dinhensis* (Hick. and A. Cam.) Barnett

219. *L. obovalifolius* (Hick. and A. Cam.) Barnett, possibly near *L. Reinwardtii*

220. *L. touranensis* (Hick. and A. Cam.) A. Cam.

MALAYAN REGION.

Borneo.

221. *L. rufus* (Seem.) A. Cam.

THE GENUS CASTANOPSIS SPACH.

The genus is entirely Asiatic, 119 species having been recorded. These may be divided into eleven more or less distinct groups.

Key to Species Groups of Castanopsis.

- A. Cupule not covering completely the single glans, shallow or deep cup-shaped, bearing scales, imbricate or arranged in rings, or entire oblique rings. 1. Group of *C. fissa* (Champ.) Rehd. and Wils., p. 183
- AA. Cupule covering the one to four glans completely.
- B. Cupule not fused with the glans.
- C. Cupules bearing small spines or tubercles or more or less entire rings.
- D. Cupule thin, comparatively small, under 2 cm. diameter, scar of glans basal. 2. Group of *C. acuminatissima* (Blume) Rehd., p. 183
- DD. Cupule thick, often large, over 2 cm. diameter, scar of glans large occupying a third or more of the glans. 10. Group of *C. inermis* (Lind.) Barnett, p. 187
- CC. Wall of cupule more or less completely hidden by simple or branched spines.
- D. Spines slender more or less completely covering the cupule.
- E. Leaves serrate usually large and coriaceous. 3. Group of *C. indica* A. DC., p. 184
- EE. Leaves usually entire (in a few species of the *C. tribuloides* group they are serrate or dentate at the apex).
- F. Cupule large over 2 cm. diameter.
- G. Leaves coriaceous.
- H. Scar of glans large often c. half height of glans.
 - i. Nerves bold. 4. Group of *C. diversifolia* (Kurz) King, p. 184
 - ii. Nerves slender. 5. Group of *C. annamensis* Hick. and A. Cam., p. 184
- HH. Scar of glans basal; lateral nerves slender. 6. Group of *C. javanica* (Blume) A. DC., p. 184
- GG. Leaves papery. 7. Group of *C. argentea* (Blume) A. DC., p. 185
- FF. Cupules small less than 2 cm. diameter. 8. Group of *C. tribuloides* (Smith) A. DC. p. 185
- DD. Spines stout branching grey-pubescent not completely covering the cupule. 9. Group of *C. armata* (Roxb.) Spach., p. 187
- BB. Cupule completely fused with the glans. 11. Group of *C. rhamnifolia* (Miq.) A. DC., p. 188

1. Group of *C. fissa* (Champ.) Rehd. and Wils.

1. *C. fissa* (Champ.) Rehd. and Wils.
2. *C. calathiformis* (Skan) Rehd. and Wils.
3. *C. cerebrina* (Hick. and A. Cam.) Barnett
4. *C. tunkinensis* (Drake) Barnett

This group forms a connecting link between this genus and *Lithocarpus*. *Castanopsis fissa* is a typical species of the genus with its cupule covering the glans and splitting at maturity, but *C. calathiformis*, with its cup-shaped cupule covering about half the glans, resembles more closely species of *Lithocarpus*. The two species are, however, very closely related and are indistinguishable in leaf and flower. *C. cerebrina* in size of cupule is intermediate between the two former species.

The main centre of distribution is Indo-China. All the species occur in French Indo-China, *C. cerebrina* and *C. tunkinensis* being endemic. *C. fissa* and *C. calathiformis* also occur in China and Thailand, the former being recorded also from Hainan and the latter from Burma.

2. Group of *C. acuminatissima* (Blume) Rehd.

5. *C. acuminatissima* (Blume) Rehd.
6. *C. brevispinula* Hick. and A. Cam.
7. *C. cuspidata* (Thunb.) Schky.
8. *C. discocarpa* Hance
9. *C. Fleuryi* Hick. and A. Cam.
10. *C. quangtriensis* Hick. and A. Cam.
11. *C. lanceaefolia* (Roxb.) Hick. and A. Cam.
12. *C. sclerophylla* (Lindl.) Schky.

This group is also well represented in French Indo-China where four of the nine species are found, *C. brevispinula*, *Fleuryi*, and *quangtriensis* being endemic. But the group as a whole is much more widely distributed than the *C. fissa* group, some species occurring in all four Asiatic regions. The type species has a wide distribution, occurring in China, Formosa, Thailand, Indo-China, and extending southwards through the Malay Peninsula to the Malay Islands and New Guinea. Another widely distributed species is *C. lanceaefolia* which is found as far west as Sikkim, in the Indian Himalaya, and extends eastwards to Upper Burma and Thailand. *C. cuspidata* and *C. sclerophylla* are restricted to the Chinese region, the latter being endemic to China. *C. discocarpa* is Malayan.

3. Group of *C. indica* A. DC.

- 13. *C. indica* A. DC.
- 14. *C. choboensis* Hick. and A. Cam.
- 15. *C. Clarkei* King
- 16. *C. Gamblei* Hick. and A. Cam.
- 17. *C. subacuminata* Hay.
- 18. *C. hystrix* A. DC.
- 19. *C. laotica* Hick. and A. Cam.
- 20. *C. taiwaniana* Hay.

This group belongs mainly to northern regions, only *C. hystrix* having been recorded from the Malay Peninsula. The type species is widely distributed from the Indian Himalaya eastwards to China, Formosa, and Hainan, and extends southwards to Thailand and French Indo-China. *C. Clarkei* is also Himalayan, extending southwards to the Indo-Chinese Peninsula. *C. subacuminata* and *C. taiwaniana* are endemic to Formosa. The remaining three species are endemic to French Indo-China.

4. Group of *C. diversifolia* (Kurz) King.

- 21. *C. diversifolia* (Kurz) King
- 22. *C. Mottleyana* King

The type species occurs in Burma, in Northern and Peninsular Thailand, and has been recorded from China. The other species is endemic to Borneo.

5. Group of *C. annamensis* Hick. and A. Cam.

- 23. *C. annamensis* Hick. and A. Cam.
- 24. *C. cambodiana* Hick. and A. Cam.
- 25. *C. nhatrangensis* Hick. and A. Cam.
- 26. *C. Oerstedii* Hick. and A. Cam.

I have not seen any of the species of this group, but from the descriptions they appear to form a connecting link between Group 4 and Group 6. All are endemic to French Indo-China.

6. Group of *C. javanica* (Blume) A. DC.

- 27. *C. javanica* (Blume) A. DC.
- 28. *C. Andersoni* Gamble
- 29. *C. catappaefolia* King
- 30. *C. costata* (Blume) A. DC.
- 31. *C. fulva* Gamble
- 32. *C. Kawakami* Hay.

33. *C. kinabaluensis* A. Cam.
34. *C. malaccensis* Gamble
35. *C. ninhoensis* Hick. and A. Cam.
36. *C. Poilanei* Hick. and A. Cam.
37. *C. Scortechinii* Gamble
38. *C. tessellata* Hick. and A. Cam.
39. *C. tibetana* Hance
40. *C. Tungurrut* (Blume) A. DC.

The main centre of distribution of the group is Malaya, nine of the fourteen species occurring in this region. Five of these are endemic to the Peninsula and two to the islands. The two non-endemic species, *C. javanica* and *C. costata*, extend northwards, the former to Lower Burma, the latter to Peninsular Thailand. The three species of Hickel and A. Camus and *C. kinabaluensis* are endemic to French Indo-China. Only two species occur in the Chinese region, *C. tibetana* in Tibet and China and *C. Kawakami* in Formosa, Hainan, and Japan.

7. Group of *C. argentea* (Blume) A. DC.

41. *C. argentea* (Blume) A. DC.
42. *C. argyrophylla* King
43. *C. borneensis* King
44. *C. castanicaarpa* (Roxb.) Spach.
45. *C. conspersispina* Merr.

This is a widely distributed group. Three of the species are Malayan. The type extends northwards from the Malay Islands to Peninsular Thailand and Lower Burma. *C. borneensis* is endemic to Borneo, *C. conspersispina* to Sumatra. The other two are northern species, *C. castanicaarpa* endemic to Eastern Bengal and Assam, while *C. argyrophylla* has its main centre of distribution in the Indo-Chinese Peninsula where it occurs in Thailand, Burma, and French Indo-China. It has also been recorded from China.

8. Group of *C. tribuloides* (Smith) A. DC.

46. *C. tribuloides* (Smith) A. DC.
47. *C. Boisii* Hick. and A. Cam.
48. *C. ceratacantha* Rehd. and Wils.
49. *C. chinensis* Hance
50. *C. Chingii* A. Cam.
51. *C. concinna* (Champ.) A. DC.
52. *C. crassifolia* Hick. and A. Cam.
53. *C. cryptoneuron* (Leveille) A. Cam.

54. *C. Delavayi* Franchet
55. *C. dongchoensis* Hick. and A. Cam.
56. *C. Eyrei* (Champ.) Tutcher
57. *C. Fabri* Hance
58. *C. Fargesii* Franchet
59. *C. Fordii* Hance
60. *C. formosana* Hay.
61. *C. Greenii* Chun
62. *C. Harmandii* Hick. and A. Cam.
63. *C. Hickelii* A. Cam.
64. *C. incana* A. Cam.
65. *C. jucunda* Hance
66. *C. nebularum* Hick. and A. Cam.
67. *C. neo-Cavalieri* A. Cam.
68. *C. ninbiensis* Hick. and A. Cam.
69. *C. orthacantha* Franchet
70. *C. pachyrachis* Hick. and A. Cam.
71. *C. platyacantha* Rehd. and Wils.
72. *C. tenuinervis* A. Cam.
73. *C. tenuispinula* Hick. and A. Cam.
74. *C. tonkinensis* Seem.
75. *C. tranninhensis* Hick. and A. Cam.
76. *C. trinervis* A. Cam.

Of the 31 species belonging to this group 21 are found in Chinese areas, 18 being endemic to China. The nine species of Hickel and A. Camus and *C. tonkinensis* are endemic to French Indo-China. The group is not represented in Malaya, but the type species which is widely distributed extends southwards through the Indo-Chinese Peninsula to Lower Burma. It occurs in the Indian Himalaya and extends eastwards to Assam, China, and Formosa.

The following species (77-82) I have not seen. From the descriptions it is not possible to place them definitely in any of the groups, but they possibly have affinity with the *tribuloides* group.

77. *C. brevispina* Hay.
78. *C. Kusanoi* Hay.
79. *C. stellato-spina* Hay.
80. *C. Lecomtei* Hick. and A. Cam.
81. *C. namdinhensis* Hick. and A. Cam.
82. *C. ouonbiensis* Hick. and A. Cam.

The first three species, all of which are endemic to Formosa, are nearly related to each other. *C. brevispina* is given as near

C. tribuloides; *C. Kusanoi* as near *C. diversifolia* (Group 4) and *C. argentea* (Group 7) but resembling *C. tribuloides* in leaf form.

The remaining three species are French Indo-Chinese, but *C. namdinhensis* has also been recorded from China and Hainan. They differ from the *tribuloides* group in having the cupule larger and the spines somewhat stronger. *C. ouonbiensis* is indehiscent although the glans is not fused with the cupule. *L. Lecomtei* is incompletely indehiscent. In this character they approach the group of *C. rhamnifolia*.

9. Group of *C. armata* (Roxb.) Spach.

- 83. *C. armata* (Roxb.) Spach.
- 84. *C. concolor* Rehd. and Wils.
- 85. *C. pachycarpa* A. Cam.
- 86. *C. purpurea* Barnett

The type species is widely distributed, occurring in the Indian Himalaya of Sikkim, extending eastwards to Eastern Bengal and Assam, and has been recorded from China, Thailand, Burma, and the Malay Peninsula. The other three are endemic species, *C. concolor* of China, *C. pachycarpa* of the Malay Peninsula, and *C. purpurea* of Thailand, where it occurs in both North-Western and Peninsular areas.

10. Group of *C. inermis* (Lindl.) Barnett.

- 87. *C. inermis* (Lindl.) Barnett
- 88. *C. arietina* Hick. and A. Cam.
- 89. *C. Hullettii* King
- 90. *C. Lamontii* Hance
- 91. *C. longipetiolata* Hick. and A. Cam.
- 92. *C. Pearsonii* Merr.
- 93. *C. Pierrei* Hance
- 94. *C. piriformis* Hick. and A. Cam.
- 95. *C. turbinata* Stapf
- 96. *C. Wilsonii* Hick. and A. Cam.

There are two centres of distribution for this group, Malaya and French Indo-China. The type species is comparatively widely distributed in Malayan areas, from the Philippines and Malay Islands through the Malay Peninsula to Burma and Peninsular Thailand. Three other species are Malayan, *C. Hullettii* endemic to the Peninsula, *C. Pearsonii* and *C. turbinata* to Borneo. The group is represented in China by the endemic *C. Lamontii*. All the

other species are French Indo-Chinese, *C. Pierrii* and *C. piriformis* also occurring in Thailand.

11. Group of *C. rhamnifolia* (Miq.) A. DC.

- 97. *C. rhamnifolia* (Miq.) A. DC.
- 98. *C. birmanica* A. Cam.
- 99. *C. Curtisii* King
- 100. *C. dispersispina* Merr.
- 101. *C. Elmeri* Merr.
- 102. *C. hainanensis* Merr.
- 103. *C. megacarpa* Gamble
- 104. *C. nephelioides* King
- 105. *C. Ridleyi* Gamble
- 106. *C. Rockii* A. Cam.
- 107. *C. Schefferiana* Hance
- 108. *C. tcheponensis* Hick. and A. Cam.
- 109. *C. Wallichii* King
- 110. *C. Woodii* Merr.

In the above list I quote both *C. Elmeri* and *C. Woodii*, but, from an examination of the type sheets in the Herbarium at Kew, I can find no difference between the two. I think *C. Elmeri* should be reduced to *C. Woodii*.

This is a typically Malayan group. It is represented in northern regions by three endemic species, *L. hainanensis* in Hainan, *C. Rockii* in China, and *C. birmanica* in Burma. *C. tcheponensis* is endemic to French Indo-China. All the others are Malayan, the type species occurring in both the Islands and the Peninsula and extending northwards into Burma.

Unplaced Species.

The following French Indo-Chinese species I have not seen nor have I been able to consult the literature.

- 111. *C. goniacantha* A. Cam.
- 112. *C. longipes* A. Cam.

Species incompletely known.

The following species have been described from immature material and it is not possible to determine their exact position.

- 113. *C. brevistella* Hay. and Kanehira. Formosa
- 114. *C. Buruana* Miq. Malay Islands
- 115. *C. Griffithii* A. Cam. (= *Q. Jenkinsii* Benth. pro parte).
Burma

116. *C. Matsudai* Hay. Formosa

117. *C. torulosa* Hick. and A. Cam. (young fruits resemble *C. Pierrei*). French Indo-China

118. *C. touranensis* Hick. and A. Cam. French Indo-China

The following species I have not seen. A. Camus (Les Chataigniers, 1929) suggests that it may be a form of *C. acuminatissima* (Group 2).

119. *C. Foxworthyi* Schky. Borneo

SUMMARY.

The three genera of oak, *Quercus* Linn., *Lithocarpus* Blume, and *Castanopsis* Spach., are represented in Eastern Asia by four hundred and eighty-five species, *Quercus* with 145, *Lithocarpus* with 221, and *Castanopsis* with 119 species.

The genus *Quercus* is divided, according to the arrangement of cupular scales, into two sections, *Lepidobalanus* and *Cyclobalanopsis*. These sections are further divided into species groups, the former into eight, the latter into seven groups. The genus *Lithocarpus* is divided by the form of the fruit into five sections, *Pasania*, *Cyclobalanus*, *Chlamydoalanus*, *Synaedrys*, and *Corylopasania*. Of these *Chlamydoalanus* and *Corylopasania* are small sections with sixteen and three species respectively. *Pasania*, by far the largest section, with one hundred and eight species, is further divided into twelve species groups, *Cyclobalanus*, with twenty-nine species, into three groups, and *Synaedrys*, with thirty-four species, into four groups. The genus *Castanopsis* is divided into eleven species groups.

For purposes of distribution Eastern Asia is divided into four main regions. These are referred to as the Indo-Burmese, Chinese, French Indo-Chinese, and Malayan regions. Notes on the distribution of the species groups are given and a detailed distribution of individual species is shown in the accompanying tables.

While each of the three genera is represented in all the four regions, the distribution of the genera is quite distinct. The genus *Quercus*, unlike the other genera, is not wholly Asiatic. The section *Lepidobalanus*, comprising a large number of species, is largely American. It is represented in Asia by comparatively few species and is absent from the Malayan region. The Asiatic species of the genus are found mainly in northern regions, with the Chinese region as the main centre. A true Malayan element is probably represented by five species of the *Q. oidocarpa* group. The number of species in Malaya is increased by some Indo-Burmese species which

have migrated southwards. The relationship between the genera *Lithocarpus* and *Castanopsis* is much closer than that between either of them and *Quercus*. In geographical distribution also these two genera resemble each other. Malayan and French Indo-Chinese regions are richest in species of *Lithocarpus*, while species of *Castanopsis* are more evenly distributed in French Indo-Chinese, Chinese, and Malayan regions. Both genera are poorly represented in the Indo-Burmese region.

The distribution of the genera is as follows:—

Total No. of Species.		Indo-Burmese.	Chinese.	French Indo-Chinese.	Malayan.
		Per cent.	Per cent.	Per cent.	Per cent.
<i>Quercus</i>	145	32 or 22	79 or 54	45 or 31	18 or 12
<i>Lithocarpus</i>	221	28 „ 13	55 „ 25	81 „ 37	85 „ 38
<i>Castanopsis</i>	119	17 „ 14	43 „ 36	48 „ 40	39 „ 33

The floras of the three northern regions (Indo-Burmese, Chinese, and French Indo-Chinese) are closely related, many of the species being common to all three. The Malayan flora is much more distinctive. Many of the species belong to groups not represented in other regions. It has been enriched by plants from other regions, the Indo-Burmese in particular. True Malayan species do not occur farther north than Lower Burma and Peninsular Thailand.

Thanks are due to the authorities at the Royal Botanic Garden, Kew, for permission to work in the Herbarium and for assistance in other ways. I am grateful also for facilities afforded me at the Botany Department of the University of Aberdeen, where much of this investigation was carried out. To the Carnegie Trust for the Universities of Scotland I am greatly indebted for a grant in aid of publication.

ADDENDUM.

Since this paper was completed and in the hands of the publishers my attention was drawn to the lately published Flora of Fukien, Metcalf (1942). The following species, given by Metcalf, I had not recorded:—

Quercus.

- Q. acutissima* Carruthers, from China and Hainan, is near *Q. serrata* Thunb., with which species it has been confused.
Q. kouangsiensis Camus. No relationship is suggested for this species.

*Lithocarpus.**L. ellipticus* Metcalf*L. Tsangii* Camus*L. uncinatus* Camus

These three species, the last from Hainan, the others from China, all belong to the group of *L. corneus* (Lour.) Rehder.

L. caudatilimbus (Merr.) Camus from Hainan. No relationship is suggested.

L. paniculatus Hand.-Mazz. from China and Hainan. No relationship is suggested.

Castanopsis.

C. argyracantha Camus belongs to the *C. tribuloides* (Smith) A. DC. group.

TABLE I.
DISTRIBUTION OF THE SPECIES OF QUERCUS IN EASTERN ASIA.
Sect. LEPIDOBALANUS.

Species.	Indo-Burmese.			Chinese.				F.I.C.	Malayan.			
	Ind.	U.B.	Th.	Ch.	Ha.	K.	F.	Jap.	L.B.	P.Th.	M.P.	M.I.
Group 1.												
<i>*ilex</i>	×	.	.	.	.	.	.	.	.	.	.	.
<i>acrodonta</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>Handeliana</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>phillyraeoides</i>	.	.	.	×	.	.	.	×	.	.	.	.
<i>setulosa</i>	.	.	×	.	.	.	.	.	×	.	.	.
<i>singuliflora</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>Wrightii</i>	.	.	.	.	.	.	.	×	.	.	.	.
<i>dilatata</i>	×	.	.	×	.	.	.	.	.	.	.	.
Group 2.												
<i>semecarpifolia</i>	×	.	×	×	.	.	.	.	.	.	.	.
<i>aquifolioides</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>longispica</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>pannosa</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>pseudo-semecarpifolia</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>senescens</i>	×	.	.	×	.	.	.	.	.	.	.	.
<i>spinosa</i>	.	.	.	×	.	.	×	.	.	.	.	.
Group 3.												
<i>Gilliana</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>cocciferoides</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>laotica</i>	.	.	.	.	.	.	.	×	.	.	.	.
<i>taliensis</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>taroensis</i>	.	.	.	.	.	.	×	.	.	.	.	.
Group 4.												
<i>Kingiana</i>	.	×	×	.	.	.	.	.	.	.	.	.
Group 5.												
<i>serrata</i>	×	×	×	×	×	×	×	×	×	.	.	.
<i>Baronii</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>Chenii</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>Moulei</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>spathulata</i>	.	.	.	×	.	.	.	.	.	.	.	.
† <i>variabilis</i>	.	.	.	×	.	×	×	.	.	.	.	.
Group 6.												
<i>aliena</i>	×	×	×	×	.	.	.	×	×	.	.	.
<i>Fabri.</i>	.	.	.	×	? ×	? ×	.	.	.	.	.	.
<i>glandulifera</i>	.	.	.	×	.	×	.	×	.	.	.	.
<i>laotungensis</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>mongolica</i>	.	.	.	×	.	×	.	×	.	.	.	.

* Also occurs in N. Africa and Asia Minor.

† Also occurs in S.E. Tibet and in Japan, but in the latter most probably in cultivation.

TABLE I—continued.

Species.	Indo-Burmese.			Chinese.					F.I.C.	Malayan.			
	Ind.	U.B.	Th.	Ch.	Ha.	K.	F.	Jap.		L.B.	P.Th.	M.P.	M.I.
<i>alienoides</i> . . .	.	.	.	.	.	x	.	.	.	.	.	.	.
<i>paucilepis</i> . . .	.	.	.	.	.	x	.	.	.	.	.	.	.
<i>pongtungensis</i> . . .	.	.	.	.	.	x	.	.	.	.	.	.	.
<i>serratooides</i> . . .	.	.	.	.	.	x	.	.	.	.	.	.	.
<i>malacotricha</i> . . .	.	.	.	x	.	.	.	.	.	.	.	.	.
<i>Stewardii</i> . . .	.	.	.	x	.	.	.	.	.	.	.	.	.
Group 7.													
<i>dentata</i> . . .	.	.	.	x	.	x	x	x	.	.	.	.	.
<i>anguste-lepidota</i> . . .	.	.	.	.	.	x	.	x	.	.	.	.	.
<i>pseudodentata</i> . . .	.	.	.	.	.	x	.	.	.	.	.	.	.
Group 8.													
<i>lanata</i> . . .	.	x	.	? x	.	.	.	.	? x	.	.	.	.
<i>Franchetii</i> . . .	.	.	.	x	.	.	.	.	.	.	.	.	.
<i>incana</i> . . .	.	x	x	? x	.	.	.	.	? x	.	.	.	.
* <i>lodicosa</i> . . .	.	x	.	.	.	.	.	.	.	.	.	.	.
<i>Engleriana</i> . . .	.	.	? x	.	x	.	.	.	.	.	.	.	.
Sect. CYCLOBALANOPSIS.													
Group 9.													
<i>glauca</i> . . .	.	x	x	.	x	.	x	x	.	.	.	.	.
<i>Augustinii</i> . . .	.	.	x	.	x	.	.	.	.	.	.	.	.
<i>bambusifolia</i> . . .	.	.	.	.	x	.	.	.	x	.	.	.	.
<i>Chevalieri</i> . . .	.	.	.	.	.	.	.	.	x	.	.	.	.
<i>Delavayi</i> . . .	.	.	.	x	.	.	.	.	.	.	.	.	.
<i>djiringensis</i> . . .	.	.	.	.	.	.	.	.	x	.	.	.	.
<i>gilva</i> . . .	.	.	.	.	x	.	x	x	.	.	.	.	.
<i>hunanensis</i> . . .	.	.	.	.	x	.	.	.	.	.	.	.	.
<i>myrsinaefolia</i> . . .	.	.	.	x	x	.	.	x	.	.	.	.	.
<i>paucidentata</i> . . .	.	.	.	.	.	.	.	x	.	.	.	.	.
<i>rupestris</i> . . .	.	.	.	.	.	.	.	.	x	.	.	.	.
<i>salicina</i> . . .	.	.	.	.	.	x	x	x	.	.	.	.	.
<i>saravanensis</i> . . .	.	.	.	.	.	.	.	.	x	.	.	.	.
<i>Sasakii</i> . . .	.	.	.	.	.	.	.	x	.	.	.	.	.
<i>Schottkyana</i> . . .	.	.	.	x	.	.	.	.	.	.	.	.	.
<i>tranninhensis</i> . . .	.	.	.	.	x	.	.	.	x	.	.	.	.
<i>xanthotricha</i> . . .	.	.	.	.	.	.	.	.	x	.	.	.	.
<i>brevistyla</i> . . .	.	.	.	.	.	.	.	.	.	.	.	x	.
<i>Miyagii</i> . . .	.	.	.	.	.	.	.	x	.	.	.	.	.
<i>stenophylloides</i> . . .	.	.	.	.	.	.	x	.	.	.	.	.	.
<i>yayeyamensis</i> . . .	.	.	.	.	.	.	.	x	.	.	.	.	.

* Also occurs in S.E. Tibet.

TABLE I—continued.

Species.	Indo-Burmese.			Chinese.					F.I.C.	Malayan.			
	Ind.	U.B.	Th.	Ch.	Ha.	K.	F.	Jap.		L.B.	P.Th.	M.P.	M.I.
Group 10.													
<i>acuta</i>	.	.	.	×	.	×	.	×	.	.	.	.	.
<i>Buergerii</i>	.	.	.	.	.	.	.	×	.	.	.	.	.
<i>Morii</i>	.	.	.	.	.	.	×	.	.	.	.	.	.
<i>nubium</i>	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>sessilifolia</i>	.	.	.	×	.	.	.	×	.	.	.	.	.
<i>Championi</i>	.	.	.	×	.	.	×	.	.	.	.	.	.
<i>Hui</i>	.	.	.	×	×	.	.	.	.	.	.	.	.
<i>Chungii</i>	.	.	.	×	×	.	.	.	.	.	.	.	.
Group 11.													
<i>semiserrata</i>	×	×	×	.	.	.	.	.	×	×	.	? ×	? ×
<i>Blakei</i>	.	.	.	×	×	.	.	.	.	.	.	.	.
<i>cambodiensis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>crassilamellata</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>Edithae</i>	.	.	.	×	×	.	.	.	? ×	.	.	.	.
<i>Elmeri</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>Fleuryi</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>glabricupula</i>	.	.	×	.	.	.	.	.	.	.	.	.	.
<i>Horsfieldii</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>langbianensis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>longistyla</i>	.	.	×	.	.	.	.	.	.	.	×	.	.
<i>pachyloma</i>	.	.	.	×	.	.	? ×	.	.	.	.	.	.
<i>patkoensis</i>	×	.	.	.	.	.	.	.	.	.	.	.	.
<i>platycalyx</i>	.	.	.	×	.	.	.	.	×	.	.	.	.
<i>quangtriensis</i>	.	.	.	.	×	.	.	.	×	.	.	.	.
<i>Ramsbottomi</i>	.	.	.	.	.	.	.	.	.	×	×	.	.
<i>tomentosicupula</i>	.	.	.	×	.	.	×	.	.	.	.	.	.
<i>turbinata</i>	.	.	.	.	.	.	.	.	×	.	.	.	×
<i>wangsaiensis</i>	.	.	.	.	.	.	.	.	.	.	×	.	.
<i>xanthoclada</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>asymmetrica</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>austrocochinchinensis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>baniensis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>blaoensis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>Camusae</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>chrysocalyx</i>	.	.	.	.	×	.	.	.	×	.	.	.	.
<i>donnaiensis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>macrocalyx</i>	.	.	.	.	×	.	.	.	×	.	.	.	.
<i>subumbilicata</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
Group 12.													
<i>lineata</i>	×	×	×	.	.	.	.	.	.	.	.	.	×
<i>braianensis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>eriolada</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>flavescens</i>	.	.	.	.	×	.	.	.	×	.	.	.	.
<i>fructiseptata</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>lamellosa</i>	×	×	.	.	.	.	.	.	.	.	.	.	.
<i>oxyodon</i>	×	×	.	×	.	.	.	.	.	.	.	.	.
<i>Rex</i>	×	×	×	×	.	.	.	.	×	.	.	.	.

TABLE I—continued.

Species.	Indo-Burmese.			Chinese.					F.I.C.	Malayan.			
	Ind.	U.B.	Th.	Ch.	Ha.	K.	F.	Jap.		L.B.	P.Th.	M.P.	M.I.
<i>vestita</i> . . .	×	×	×	.	.	.	.	.	×	×	.	.	.
<i>chapensis</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>Dussaudii</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>Gambleana</i> . . .	×	.	.	.	.	.	.	.	.	.	.	.	.
Group 13.													
<i>Helperiana</i> . . .	×	×	×	×	×	.	.	.	×	×	.	.	.
<i>dilacerata</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>Kerrii</i> . . .	.	?×	×	.	.	.	.	.	×	.	∇	.	.
<i>mespilifolia</i> . . .	×	×	.	.	.	.	.	.	×	.	.	.	.
<i>Thorelii</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
Group 14.													
<i>Brandisiana</i> . . .	.	×	×	.	.	.	.	.	.	.	.	.	.
Group 15.													
<i>oidocarpa</i> . . .	.	.	.	.	.	.	.	.	.	×	×	×	×
<i>argentata</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	×
<i>Hendersoniana</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>Jenseniana</i> . . .	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>lenticellata</i> . . .	.	.	×	.	.	.	.	.	.	.	.	.	.
<i>Lowii</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>nivea</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	×

v = var. *pubescens*.

TABLE II.

DISTRIBUTION OF THE SPECIES OF LITHOCARPUS IN EASTERN ASIA.

Sect. PASANIA.

Species.	Indo-Burmese.			Chinese.					F.I.C.	Malayan.			
	Ind.	U.B.	Th.	Ch.	Ha.	K.	F.	Jap.		L.B.	P.Th.	M.P.	M.I.
Group 1.													
<i>Scortechinii</i> . . .	.	.	.	.	.	.	.	.	.	×	.	×	.
<i>Arecus</i> . . .	.	.	.	.	.	.	.	.	.	×	.	.	.
<i>cyrtocarpus</i> . . .	.	.	.	.	.	.	.	.	.	×	.	.	.
Group 2.													
<i>lappaceus</i> . . .	×	×	×	.	.	.	.	.	.	.	.	×	.
<i>Bonnetii</i> . . .	.	.	.	.	.	.	.	.	.	×	.	.	.
<i>echinocarpus</i> . . .	.	.	.	.	.	.	.	.	.	×	.	.	.
<i>echinophorus</i> . . .	.	.	.	.	.	.	.	.	.	×	.	.	.
<i>Garrettianus</i> . . .	.	.	×	.	.	.	.	.	.	×	.	.	.
<i>hypophoeniceus</i> . . .	.	.	.	.	.	.	.	.	.	×	.	.	.
<i>Kingianus</i> . . .	.	.	.	.	.	.	.	.	.	?	×	.	.
<i>longispinus</i> . . .	.	.	.	.	.	.	.	.	.	.	×	.	.
<i>recurvatus</i> . . .	.	.	×	.	.	.	.	.	.	.	.	.	.
<i>reflexus</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>Rodgerianus</i> . . .	.	.	.	.	.	.	.	.	.	×	.	.	.
<i>Skanianus</i> . . .	.	.	.	×	×	.	.	.	.	.	.	.	.
<i>Wrayii</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	.
Group 3.													
<i>sundaicus</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	×
<i>celebicus</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>conocarpus</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	×
<i>dasystachyus</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	×
<i>hystrix</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	×
<i>lampongus</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	×
<i>Winklerianus</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>grandifrons</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>elephantum</i> . . .	.	.	.	.	.	.	.	.	.	×	.	.	.
<i>gigantophyllus</i> . . .	.	.	.	.	.	.	.	.	.	×	.	.	.
<i>pseudosundaicus</i> . . .	.	.	.	.	.	.	.	.	.	×	.	.	.
<i>Finetii</i> . . .	.	.	.	.	.	.	.	.	.	×	.	.	.
Group 4.													
<i>fenestratus</i> . . .	×	×	×	×	×	.	.	.	.	×	.	?	×
<i>acuminatus</i> . . .	×	.	.	.	.	.	.	.	.	.	.	.	.
<i>Cottonii</i> . . .	.	×	.	.	.	.	.	.	.	.	.	.	.
<i>Craibianus</i> . . .	.	.	×	.	.	.	.	.	.	.	.	.	.
<i>dealbatus</i> . . .	×	.	×	×	.	.	.	.	.	×	.	.	.
<i>elaeagnifolius</i> . . .	.	.	.	.	×	.	.	.	.	?	×	.	.
<i>Elizabethae</i> . . .	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>Handelianus</i> . . .	.	.	.	.	×	.	.	.	.	.	.	.	.
<i>kemmaratensis</i> . . .	.	.	.	.	.	.	.	.	.	×	.	.	.
<i>pycnostachyus</i> . . .	.	.	.	.	.	.	.	.	.	×	.	.	.

TABLE II—continued.

Species.	Indo-Burmese.			Chinese.					F.I.C.	Malayan.			
	Ind.	U.B.	Th.	Ch.	Ha.	K.	F.	Jap.		L.B.	P.Th.	M.P.	M.L.
<i>rhabdostachyus</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>tephrocarpus</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>triqueter</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>variolosus</i> . . .	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>intermedius</i> . . .	.	×	×	.	.	.	.	.	.	.	×	.	.
<i>braianensis</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>synbalanos</i> . . .	.	.	.	×	.	.	.	.	.	.	.	.	.
Group 5.													
<i>glabrus</i> . . .	.	.	.	×	.	.	.	×	.	.	.	.	.
<i>brunneus</i> . . .	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>dodonaeifolius</i> . . .	.	.	.	.	.	.	×	.	.	.	.	.	.
<i>edulis</i> . . .	.	.	.	.	.	.	.	×	.	.	.	.	.
<i>elatus</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>eucalyptifolius</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>formosanus</i> . . .	.	.	.	.	.	.	×	.	.	.	.	.	.
<i>Hancei</i> . . .	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>Harlandii</i> . . .	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>Irwinii</i> . . .	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>iteaphyllus</i> . . .	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>Krempfii</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>Mairei</i> . . .	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>naiadarum</i> . . .	.	.	.	×	✓	.	.	.	.	.	.	.	.
<i>silvicularum</i> . . .	.	.	.	?	×	✓	.	.	×	.	.	.	.
<i>taioensis</i> . . .	.	.	.	.	.	.	✓	.	.	.	.	.	.
<i>ternaticupulus</i> . . .	.	.	.	.	.	.	✓	.	.	.	.	.	.
<i>viridis</i> . . .	.	×	.	✓	.	.	.	.	.	.	.	.	.
Group 6.													
<i>Kunstleri</i> . . .	.	.	.	.	.	.	.	.	×	.	.	×	×
<i>ochraceus</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>borneensis</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	×
Group 7.													
<i>Falconeri</i> . . .	.	.	.	.	.	.	.	.	.	×	×	×	.
<i>Amherstianus</i> . . .	.	.	.	.	.	.	.	.	.	×	.	.	.
<i>bancanus</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>craterophorus</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>rufescens</i> . . .	.	.	.	.	.	.	.	.	.	.	×	.	.
<i>scyphiger</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	×
Group 8.													
<i>Curtisii</i> . . .	.	.	.	.	.	.	.	.	.	.	×	×	? ×
<i>cerifer</i> . . .	.	.	.	.	.	.	.	.	✓	.	.	.	.
Group 9.													
<i>spicatus</i> . . .	×	×	×	×	.	.	.	.	×	×	×	×	×
<i>annamensis</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>bacgiangensis</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.

TABLE II—continued.

Species.	Indo-Burmese.			Chinese.					F.I.C.	Malayan.			
	Ind.	U.B.	Th.	Ch.	Ha.	K.	F.	Jap.		L.B.	P.Th.	M.P.	M.I.
<i>brevicaudatus</i>	.	.	.	×	.	.	×	.	×	.	.	.	.
<i>chittagongus</i>	×	.	.	.	.	.	.	.	×	.	.	.	.
<i>Ducampii</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>erythrocarpus</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>Henryi</i>	.	.	.	×	×	.	.	.	.	.	.	×	.
<i>Kawakamii</i>	.	.	.	.	.	.	×	.	.	.	.	.	.
<i>megalophyllus</i>	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>Pierrei</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>sabulicolus</i>	.	.	.	.	.	.	.	×	×	.	.	.	.
<i>seishoi</i>	.	.	.	.	.	.	×	.	.	.	.	.	.
<i>auriculatus</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>bassacensis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>parvulus</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
Sub-group.													
<i>Lindleyanus</i>	.	×	×	.	.	.	.	.	×	.	.	.	.
<i>Harmandii</i>	.	.	×	.	.	.	.	.	×	.	.	.	.
Group 10.													
<i>Thomsoni</i>	.	×	×	.	.	.	.	.	×	.	.	.	.
<i>litseifolius</i>	.	.	.	.	×	.	.	.	.	.	.	.	.
<i>mucronatus</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>vestitus</i>	.	.	.	×	.	.	.	.	×	.	.	.	.
<i>Wallichianus</i>	.	.	.	.	.	.	.	.	.	.	×	×	.
Group 11.													
<i>polystachyus</i>	.	×	×	.	.	.	.	.	×	?×	.	.	.
<i>farinulentus</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
Group 12.													
* <i>pallidus</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>Carolinae</i>	.	.	.	×	.	.	.	.	.	.	.	.	×
<i>crassinervius</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>daphnoideus</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>dolichocarpus</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
* <i>Havilandii</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>monticolus</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>pruinosis</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>pseudo-moluccus</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
Sect. CYCLOBALANUS.													
Group 13.													
<i>Reinwardtii</i>	.	.	.	.	.	.	.	.	×	.	?×	.	×
<i>Cantleyanus</i>	.	.	×	.	.	.	.	.	.	×	×	×	.
<i>longipedicellatus</i>	.	.	.	.	.	.	.	.	×	.	.	.	.

* These species are also recorded from Luzon in the Philippines.

TABLE II—continued.

Species.	Indo-Burmese.			Chinese.					F.I.C.	Malayan.			
	Ind.	U.B.	Th.	Ch.	Ha.	K.	F.	Jap.		L.B.	P.Th.	M.P.	M.I.
<i>magneinii</i>	×	.	.	.	.	.	.	.	×	.	.	.	.
<i>poculiformis</i>	.	.	.	.	.	.	.	.	×	.	.	.	×
<i>sootepensis</i>	.	.	×	.	.	.	.	.	.	.	×	.	.
<i>tenuinervis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
Group 14.													
<i>cyrtorhynchus</i>	.	.	.	.	.	.	.	.	.	.	.	×	×
* <i>Bennettii</i>	.	.	.	.	.	.	.	.	.	.	.	×	×
<i>clathratus</i>	.	.	.	.	.	.	.	.	.	.	.	×	×
* <i>Clementianus</i>	.	?×	.	.	.	.	.	.	.	.	?×	×	.
<i>Eichleri</i>	.	.	.	.	.	.	.	.	.	.	?×	×	×
<i>Ewyckii</i>	.	.	.	.	.	.	.	.	.	.	.	×	×
<i>heliciiformis</i>	.	.	.	.	.	.	.	.	.	.	.	×	×
<i>Rangerianus</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>rassus</i>	.	.	.	.	.	.	.	.	.	.	.	×	×
<i>Ridleyanus</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>Syningtonianus</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>Wenzigianus</i>	.	.	.	.	.	.	.	.	.	.	.	×	×
Group 15.													
<i>Omalokos</i>	.	.	.	.	.	.	.	.	.	×	×	×	×
<i>costatus</i>	.	.	.	.	.	.	.	.	.	.	.	×	×
<i>cyclophorus</i>	.	.	.	.	.	.	.	.	.	.	×	×	×
<i>Diepenhorstii</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>Dunnii</i>	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>lampadarius</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>lucidus</i>	.	.	.	.	.	.	.	.	.	.	.	×	?×
<i>platycarpus</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>rajah</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>Teysmannii</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
Sect. CHLAMYDOBALANUS.													
Group 16.													
<i>encleisacarpus</i>	.	.	.	.	.	.	.	.	.	.	×	×	×
<i>aggregatus</i>	.	.	×	.	.	.	.	.	.	.	.	.	.
<i>attenuatus</i>	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>Blumeanus</i>	.	.	.	.	.	.	.	.	.	.	?×	×	×
<i>confragosus</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>echinifer</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>Macphailii</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>pattaniensis</i>	.	.	.	.	.	.	.	.	.	.	×	.	.
<i>Robinsonii</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>stenopus</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>indutus</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>coinhensis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.

* These species are also recorded from Luzon in the Philippines.

TABLE II—continued.

Species.	Indo-Burmese.			Chinese.					F.I.C.	Malayan.			
	Ind.	U.B.	Th.	Ch.	Ha.	K.	F.	Jap.		L.B.	P.Th.	M.P.	M.I.
<i>Paviei</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>Rouletii</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>sphaerocarpus</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>trachycarpus</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
Sect. SYNAEDRYS.													
Group 17.													
<i>xylocarpus</i>	×	.	.	.	.	.	.	.	.	.	.	.	.
<i>annamitorum</i>	×	.	.	.	.	.	.	.	×	.	.	.	.
<i>Mitroyi</i>	×	.	.	.	.	.	.	.	.	.	.	.	.
<i>Parkinsonii</i>	.	×	.	.	.	.	.	.	.	.	.	.	.
<i>Rosthornii</i>	.	.	.	×	.	.	.	.	.	.	.	.	.
Group 18.													
<i>corneus</i>	.	.	.	×	×	.	.	.	×	.	.	.	×
<i>comptus</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>Fordianus</i>	.	.	.	×	×	.	.	.	×	.	.	.	.
<i>hemisphaericus</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>lycoperdon</i>	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>magnificus</i>	.	×	.	.	.	.	.	.	.	.	.	.	.
<i>pachyphyllus</i>	×	×	.	.	.	.	.	.	.	.	.	.	.
<i>pulcher</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>rotundatus</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>uvariifolius</i>	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>pseudoplatycarpus</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
Group 19.													
<i>truncatus</i>	×	×	×	.	.	.	.	.	×	.	.	.	.
<i>amygdalifolius</i>	.	.	.	×	×	.	×	.	.	.	.	.	.
<i>Balansae</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>baviensis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
* <i>castanopsisifolius</i>	.	×	.	.	.	.	×	.	.	.	.	.	.
<i>cleistocarpus</i>	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>laoticus</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>megastachyus</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>Ollus</i>	×	.	.	.	.	.	.	.	.	.	.	.	.
<i>pachycarpus</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>Hendersonianus</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
Group 20.													
<i>javensis</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>Beccarianus</i>	.	.	.	.	.	.	.	.	.	.	.	×	×
<i>Burkiliti</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>Maingayi</i>	.	.	.	.	.	.	.	.	.	.	.	×	.

* The Burmese specimen is a new form—*f. birmanica* A. Cam.

TABLE II—continued.

Species.	Indo-Burmese.			Chinese.					F.I.C.	Malayan.			
	Ind.	U.B.	Th.	Ch.	Ha.	K.	F.	Jap.		L.B.	P.Th.	M.P.	M.I.
<i>scutigera</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>subnuciferus</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	×
<i>pyriformis</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	×
Group 21.													
<i>nhatrangensis</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>proboscidius</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>tubulosus</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.

TABLE III.
DISTRIBUTION OF THE SPECIES OF CASTANOPSIS IN ASIA.

Species.	Indo-Burmese.			Chinese.					F.I.C.	Malayan.			
	Ind.	U.B.	Th.	Ch.	Ha.	K.	F.	Jap.		L.B.	P.Th.	M.P.	M.I.
Group 1.													
<i>fissa</i>	.	.	.	×	×	×	.	.	.	×	.	.	.
<i>calathiformis</i>	.	×	×	×	.	.	.	.	.	×	.	.	.
<i>cerebrina</i>	.	.	.	.	.	.	.	.	.	×	.	.	.
<i>tunkinensis</i>	.	.	.	.	.	.	.	.	.	×	.	.	.
Group 2.													
* <i>acuminatissima</i>	.	.	×	×	.	.	×	.	×	.	.	×	×
<i>brevispinula</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>cuspidata</i>	.	.	.	×	.	×	×	×	.	.	.	.	.
<i>discocarpa</i>	.	.	.	.	.	.	.	.	.	.	×	×	.
<i>Fleuryi</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>quangtrienensis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>lanceaefolia</i>	×	×	×	.	.	.	.	.	.	.	.	.	.
<i>sclerophylla</i>	.	.	.	×	.	.	.	.	.	.	.	.	.
Group 3.													
<i>indica</i>	.	×	×	×	×	.	×	.	×	.	.	.	.
<i>choboensis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>Clarkei</i>	.	×	×	.	.	.	.	.	×	.	.	.	.
<i>Gamblei</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>subacuminata</i>	.	.	.	.	.	.	×	.	.	.	.	.	.
<i>hystrix</i>	.	×	×	×	.	.	.	.	×	.	?	×	.
<i>laotica</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>taiwaniana</i>	.	.	.	.	.	.	×	.	.	.	.	.	.
Group 4.													
<i>diversifolia</i>	.	.	×	×	×	.	.	.	.	.	×	.	.
<i>Mottleyana</i>	.	.	.	.	.	.	.	.	.	.	.	.	×
Group 5.													
<i>annamensis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>cambodiana</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>nhatrangensis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>Oerstedii</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
Group 6.													
<i>javanica</i>	.	.	.	.	.	.	.	.	?	×	×	.	×
<i>Andersoni</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>catappaefolia</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>costata</i>	.	.	.	.	.	.	.	.	.	.	×	×	×
<i>fulva</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>Kawakamii</i>	.	.	.	.	×	.	×	×	.	.	.	×	.
<i>kinabaluensis</i>	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>malaccensis</i>	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>ninhhoensis</i>	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Poilanei</i>	.	.	.	.	.	.	.	.	×	.	.	.	.

* Also in New Guinea.

TABLE III—continued.

Species.	Indo-Burmese.			Chinese.				F.I.C.	Malayan.			
	Ind.	U.B.	Th.	Ch.	Ha.	K.	F.	Jap.	L.B.	P.Th.	M.P.	M.I.
<i>Scortechinii</i>	.	.	.	.	.	.	.	.	.	.	×	.
<i>tessellata</i>	.	.	.	.	.	.	.	.	.	.	.	.
* <i>tibetana</i>	.	.	.	×	.	.	.	.	×	.	.	.
<i>Tungurrit</i>	.	.	.	.	.	.	.	.	.	.	.	×
Group 7.												
<i>argentea</i>	.	.	.	.	.	.	.	.	.	?	×	×
<i>argyrophylla</i>	.	×	×	×	.	.	.	.	×	×	.	.
<i>borneensis</i>	.	.	.	.	.	.	.	.	.	.	.	×
<i>castanicaarpa</i>	×	.	.	.	.	.	.	.	.	.	.	.
<i>conspersispina</i>	.	.	.	.	.	.	.	.	.	.	.	×
Group 8.												
<i>tribuloides</i>	×	×	×	×	×	.	×	.	×	×	.	.
<i>Boisii</i>	.	.	.	.	.	.	.	.	×	.	.	.
<i>ceratacantha</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>chinensis</i>	.	.	.	×	×	.	.	.	×	.	.	.
<i>Chingii</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>concinna</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>crassifolia</i>	.	.	.	.	.	.	.	.	×	.	.	.
<i>cryptoneuron</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>Delavayi</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>dongchoensis</i>	.	.	.	.	.	.	.	.	×	.	.	.
<i>Eyrei</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>Fabri</i>	.	.	.	×	×	.	.	.	.	.	.	.
<i>Fargesii</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>Fordii</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>formosana</i>	.	.	.	.	×	.	×	.	.	.	.	.
<i>Greenii</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>Harmandii</i>	.	.	.	.	.	.	.	.	×	.	.	.
<i>Hickelii</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>incana</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>jucunda</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>nebularam</i>	.	.	.	.	.	.	.	.	×	.	.	.
<i>neo-Cavaleri</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>ninbienensis</i>	.	.	.	.	.	.	.	.	×	.	.	.
<i>orthacantha</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>pachyrachis</i>	.	.	.	.	.	.	.	.	×	.	.	.
<i>platyacantha</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>tenuinervis</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>tenuispinula</i>	.	.	.	.	.	.	.	.	×	.	.	.
<i>tonkinensis</i>	.	.	.	.	.	.	.	.	×	.	.	.
<i>tranninhensis</i>	.	.	.	.	.	.	.	.	×	.	.	.
<i>trinervis</i>	.	.	.	×	.	.	.	.	.	.	.	.
<i>brevispina</i>	.	.	.	.	.	.	×	.	.	.	.	.
<i>Kusanoi</i>	.	.	.	.	.	.	×	.	.	.	.	.
<i>stellato-spina</i>	.	.	.	.	.	.	×	.	.	.	.	.
<i>Lecomtei</i>	.	.	.	.	.	.	.	.	×	.	.	.

* Also in Tibet.

TABLE III—continued.

Species.	Indo-Burmese.			Chinese.					F.I.C.	Malayan.			
	Ind.	U.B.	Th.	Ch.	Ha.	K.	F.	Jap.		L.B.	P.Th.	M.P.	M.I.
<i>namdinhensis</i> . . .	.	.	.	×	×	.	.	.	×	.	.	.	.
<i>ouonbiensis</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
Group 9.													
<i>armata</i> . . .	×	×	×	×	.	.	.	.	.	.	.	×	.
<i>concolor</i> . . .	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>pachycarpa</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>purpurea</i> . . .	.	.	×	.	.	.	.	.	.	.	×	.	.
Group 10.													
* <i>inermis</i> . . .	.	.	.	.	.	.	.	.	.	×	×	×	×
<i>arietina</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>Hullettii</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>Lamontii</i> . . .	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>longipetiolata</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>Pearsonii</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>Pierrei</i> . . .	.	.	×	.	.	.	.	.	×	.	×	.	.
<i>piriformis</i> . . .	.	.	×	.	.	.	.	.	×	.	×	.	.
<i>turbinata</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>Wilsonii</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
Group 11.													
<i>rhamnifolia</i> . . .	.	.	.	.	.	.	.	.	.	×	.	×	×
<i>birmanica</i> . . .	.	×	.	.	.	.	.	.	.	.	.	.	.
<i>Curtisii</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>dispersispina</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>Elmeri</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	×
<i>hainanensis</i> . . .	.	.	.	.	×	.	.	.	.	.	.	.	.
<i>megacarpa</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>nephelioides</i> . . .	.	.	.	.	.	.	.	.	.	.	?	×	.
<i>Ridleyi</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>Rockii</i> . . .	.	.	.	×	.	.	.	.	.	.	.	.	.
<i>Schefferiana</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	×
<i>tcheponensis</i> . . .	.	.	.	.	.	.	.	.	×	.	.	.	.
<i>Wallichii</i> . . .	.	.	.	.	.	.	.	.	.	.	.	×	.
<i>Woodii</i> . . .	.	.	.	.	.	.	.	.	.	.	.	.	×

* Also in the Philippines.

CONTENT OF VITAMIN C (1-ASCORBIC ACID) IN ARCTIC PLANTS.

By KAARE RODAHL (Institute of Physiology, University of Oslo).

(Read 15th June 1944.)

During the period from July 1939 to August 1940 an investigation was carried out in North-East Greenland under the auspices of the University of Oslo. One of the problems studied was the ascorbic acid content of Arctic flora. This paper contains the results of chemical determination of ascorbic acid in a series of Greenland plants.

Technique.—For determination of vitamin C in plant tissue a modification of the method of Tillmans was used. 1.5 grams plant tissue was ground in a mortar, adding 5 per cent. metaphosphoric acid for extraction of the ascorbic acid. The liquid was filtered and diluted to a certain volume (usually 100 c.c.). 10–25 c.c. of this solution were then titrated against 2.6 dichlorophenol-indophenol to a faint pink colour. In several cases it was necessary to filter through cotton wool. In some cases the extract itself had a strong pink colour and the method mentioned could not be used. In those cases the method of Emmerie and Van Eckelen was used (1). (After extraction with trichloroacetic acid the liquid was neutralized with calcium carbonate and mercuriacetate was added, and filtered through a Buchner funnel. The solution was saturated with hydrogen sulphide and allowed to stand over night. The hydrogen sulphide was removed by bubbling nitrogen through the liquid and the colourless solution titrated against 2.6-dichlorophenol-indophenol.) A series of analyses were carried out on each species.

Specimens of the plants examined were preserved for botanical examination to determine the species.

The technique mentioned above required a rather well-equipped laboratory, which had to be built in the Arctic at the latitude of 74° 30' N. For this purpose a trapper's hut at Revet, Clavering Island, was placed at my disposal by the Norwegian Corporation A/S Arktisk Naringsdrift, Oslo. The room was built with double panel walls and covered with tarred wall-paper. The outside walls were protected by earth from the ground to the roof. Special equipment suitable for the Arctic conditions had to be made, such as hand centrifuges, hand pumps, etc. The main difficulty was to protect the chemicals and solutions from the extremely low temperature in the middle of the winter (sometimes -50° C.), and the room temperature at times went down to -25° C. during the night.

Results.—The data are tabulated in Table I.

TABLE I.
ASCORBIC ACID CONTENT IN COMMON GREENLAND PLANTS.

Plant.	Part of Plant Analyzed.	Station.	Date of Analysis.	Mg. Ascorbic Acid per 100 g.		
				Max.	Min.	Mean.
<i>Papaver radiculatum</i> Rottb.	Whole plant	Revet	26/8/39	..	..	1.3
"	Whole plant	Revet	30/8/39	..	..	5.0
"	Leaves	Revet	6/7/40	9.2	4.4	6.8
"	Stems	Revet	6/7/40	..	..	2.8
"	Flowers	Revet	7/7/40	6.9	6.5	6.7
<i>Honckenya peploides</i> (L.) Ehrh.	Flowers	Revet	30/7/40	..	..	73.8
"	Leaves	Revet	30/7/40	60.0	50.0	55.0
"	Stems	Revet	30/7/40	..	..	15.0
"	Whole plant	Revet	26/8/39	26.7	21.9	24.3
"	Whole plant	Revet	1/9/39	13.9	12.6	13.2*
"	Whole plant	Revet	30/10/39	..	..	4.1
"	Whole plant	Revet	31/12/39	4.9	4.8	4.9
"	Whole plant	Revet	30/4/40	1.7	1.5	1.6
"	Whole plant	Revet	27/5/40	..	..	0.5†
"	Whole plant	Revet	30/7/40	..	..	47.9
"	Buds	Revet	27/5/40	..	..	0.5
"	Buds	Revet	17/6/40	30.0	29.8	29.9
"	Buds	Revet	2/7/40	80.0	53.6	63.7
"	Buds	Revet	30/7/40	60.0	50.0	55.0
<i>Stellaria humifusa</i> Rottb. or <i>longipes</i> Goldie.	Whole plant	Revet	26/8/39	68.2	50.0	59.1
<i>Rumex Acetosella</i> L.	Whole plant	Revet	30/8/39	..	..	12.0
<i>Eriophorum callitrix</i> C. A. Mey.	Whole plant	Revet	30/8/39	..	..	17.0
"	Whole plant	Revet	13/9/39	..	..	4.1*
"	Whole plant	Revet	15/9/39	..	..	1.5
<i>Cerastium alpinum</i> L.	Whole plant	Revet	13/9/39	42.4	42.0	42.2
"	Leaves	Revet	27/7/40	62.5	58.1	60.3
"	Stems	Revet	27/7/40	34.0	31.9	32.0
<i>Poa glauca</i> Vahl	Whole plant	Revet	13/9/39	..	..	11.6
<i>Alopecurus alpinus</i> Sm.	Whole plant	Revet	13/9/39	44.2	37.6	40.9
"	Leaves	Revet	29/7/40	105.0	62.5	83.7
"	Stems	Revet	29/7/40	46.0	32.0	39.0
<i>Saxifraga oppositifolia</i> L.	Whole plant	Revet	10/6/40	..	..	54.0
<i>Dryas octopetala</i> L.	Whole plant	Revet	24/6/40	..	..	243.4
"	Stems	Revet	24/6/40	..	..	200.0
"	Flowers	Revet	24/6/40	..	..	180.0
<i>Cassiope tetragona</i> (L.) Don.	Whole plant	Revet	8/7/40	150.4	120.0	148.8
<i>Arnica alpina</i> Laest	Leaves	Tyrollerfj	11/7/40	..	..	4.8
"	Stems	Tyrollerfj	11/7/40	..	..	3.6
<i>Potentilla nivea</i> L.	Leaves	Revet	12/7/40	330.0	295.0	314.3
<i>Epilobium latifolium</i> L.	Leaves	Revet	17/7/40	132.5	132.5	132.5
<i>Lychnis triflora</i> R.Br.	Leaves	Revet	20/7/40	108.8	80.0	94.4
<i>Pedicularis hirsuta</i> L.	Leaves	Revet	22/7/40	..	..	22.5
<i>Armeria vulgaris</i> Willd.	Leaves	Revet	22/7/40	195.0	128.8	165.2
"	Stems	Revet	22/7/40	135.4	105.0	119.7
<i>Saxifraga cernua</i> L.	Leaves	Revet	2/8/40	92.5	80.8	86.6
"	Stems	Revet	2/8/40	..	..	60.0

* Frost appeared 13th September 1939.

† Fresh buds just come out.

TABLE I.—*continued*.

Plant.	Part of Plant Analyzed.	Station.	Date of Analysis.	Mg. Ascorbic Acid per 100 g.		
				Max.	Min.	Mean.
<i>Salix</i> sp. (Arctic wil- low).	Buds	Revet	31/1/40	29.9	21.7	25.8
"	Buds	Revet	6/2/40	27.3	26.0	26.7
"	Buds	Revet	28/3/40	19.2	16.6	17.9
"	Buds	Revet	3/6/40	..	..	30.0
"	Stems	Revet	29/3/40	37.2	35.0	36.1
"	Stems	Revet	4/6/40	21.9	21.9	21.9
"	Stems	Revet	25/6/40	72.0	58.0	65.0
"	Stems	Revet	31/7/40	62.5	60.0	61.2
"	Leaves	Revet	25/6/40	230.7	221.0	225.8
"	Leaves	Revet	13/7/40	..	..	132.6
"	Leaves	Revet	16/7/40	92.5	90.0	90.8
"	Leaves	Revet	31/7/40	222.5	162.5	192.5
<i>Betula nana</i> L. .	Buds, just come out	Revet	1/5/40	..	..	9.0
"	Buds, fresh green	Revet	4/6/40	..	..	50.0
"	Leaves	Revet	2/7/40	232.0	205.0	218.5
"	Leaves	Revet	1/8/40	200.0	197.5	198.7
"	Leaves, veins	Revet	1/5/40	..	..	traces
"	Stems	Revet	1/5/40	..	..	8.6
"	Stems	Revet	4/6/40	..	..	10.0
"	Stems	Revet	2/7/40	14.0	13.0	13.0
"	Stems	Revet	1/8/40	..	..	8.8
<i>Empetrum nigrum</i> L..	Branches	Tyrollerfj	1/9/39	..	..	46.8
Mushroom (3 various kinds).	Whole fungus	Revet	1/11/39	..	..	0.0
"	Whole fungus	Revet	31/7- 25/9/39	2.3	0.4	1.0
<i>Alaria</i> sp. .	Whole plant	Youngsund	7/9/39	5.2	4.4	4.8
"	Whole plant	Revet	16/9/39	6.6	5.5	6.1
"	Roots and stems	Revet	16/9/39	..	..	12.0
"	Roots	Revet	16/9/39	..	..	20.6
"	Whole plant, dried	Revet	16/11/39	..	..	1.4
<i>Fucus</i> sp. .	Whole plant	Revet	16/9/39	16.7	12.0	14.4
"	Whole plant	Revet	16/11/39	..	..	3.3
"	Whole plant, dried	Revet	21/6/39	2.9	2.9	2.9

From this table it is evident that several of the plants common in Greenland are very rich in ascorbic acid, and used as a source of that vitamin there should be no reason to suffer from scurvy in this region, even without supplies of fruits from more temperate zones.

Some of the plants I have eaten myself, such as *Honckenya peploides*, *Rumex Acetosella*, seaweed, and buds of *Salix* sp., without harmful effects.

From the autumn 1939 to the autumn 1940 a consecutive series of analyses was made of the most important plants. The results are tabulated as follows:—

TABLE II.

SEASONAL VARIATIONS IN RELATION TO THE ASCORBIC ACID CONTENT OF *HONCKENYA PEPLIOIDES*.

(A) *Whole Plant.*

August 26,	1939	.	.	24.3 mg. per cent.	
September 1,	"	.	.	13.2 "	" " (Frost appeared
October 30,	"	.	.	4.1 "	" " September 13,
December 31,	"	.	.	4.9 "	" " 1939.)
April 30,	1940	.	.	1.6 "	" " "
May 27,	"	.	.	0.5 "	" " "
July 30,	"	.	.	47.9 "	" " "

(B) *Buds.*

May 27,	1940	.	.	0.5 mg. per cent.
June 17,	"	.	.	29.9 " " "
July 2,	"	.	.	63.7 " " "
July 30,	"	.	.	55.0 " " "

On 27th May the fresh buds had just come out, but still the ascorbic acid content was very low.

TABLE III.

SEASONAL VARIATIONS OF THE ASCORBIC ACID CONTENT IN *SALIX* SP.

(A) *Buds.*

January 31, 1940	.	.	25.8 mg. per cent.
February 6,	"	.	26.7 " " "
March 28,	"	.	17.9 " " "
June 3,	"	.	30.0 " " "

(B) *Stems.*

March 29,	1940	.	.	36.1 mg. per cent.
June 4,	"	.	.	21.9 " " "
June 25,	"	.	.	65.0 " " "
July 31,	"	.	.	61.2 " " "

(C) *Leaves.*

June 25,	1940	.	.	225.8 mg. per cent.
July 13,	"	.	.	132.6 " " "
July 16,	"	.	.	90.8 " " "
July 31,	"	.	.	102.5 " " "

It is interesting that buds of *Salix* sp. (Arctic willow) which is the main food for the musk ox (and ptarmigan) are comparatively rich in ascorbic acid even in winter time (25.8 mg. per cent. on 31st January).

TABLE IV.

SEASONAL VARIATIONS OF THE ASCORBIC ACID CONTENT IN *BETULA NANA* (DWARF BIRCH).

(A) *Buds and Leaves.*

May 1,	1940	.	.	9.0 mg. per cent.	Buds just out.
June 4,	"	.	.	50.0 " " "	Fresh green buds.
July 2,	"	.	.	218.5 " " "	Fresh green leaves.
August 1,	"	.	.	198.7 " " "	Fresh green leaves.
May 1,	"	.	.	0.0 " " "	Withered leaves.

(B) *Stems.*

May 1,	1940	.	.	8.6 mg. per cent.
June 4,	"	.	.	10.0 " " "
July 2,	"	.	.	13.0 " " "
August 1,	"	.	.	8.8 " " "

From the foregoing tables it will be observed that there are considerable seasonal variations in the ascorbic acid content of the plants examined. Höygaard and Rasmussen (2) examined during the expedition to Angmagssalik, S.E. Greenland, 1936-37, a number of phanerogams and algæ (*Sedum roseum*, *Salix* sp., *Taraxacum officinale*, *Archangelica officinalis*, *Empetrum nigrum*, *Alaria* sp., *Rhodymenia palmata*, *Fucus* sp., and *Ascophyllum nodosum*) by the same technique as applied by the author in N.E. Greenland, 1939-40, and it appears from the results that the ascorbic acid content is generally higher in the plants from Revet, N.E. Greenland (lat. 74° N.), as compared with the same plants in Angmagssalik, S.E. Greenland (lat. 66° N.).

TABLE V.

Species.	Høygaard and Rasmussen, Angmagssalik, Lat. 66° N. Mg. per cent. Ascorbic Acid.	Revet, Lat. 74° N. Mg. per cent. Ascorbic Acid.
<i>Empetrum nigrum</i> .	9	47
<i>Salix</i> sp. . . .	18	20-225
<i>Alaria</i> sp. . . .	45	5-20
<i>Fucus</i> sp. . . .	13	14

It is known that marine algæ have been used as food in Japan, China, Hawaii, and Iceland. Large quantities of algæ are consumed by the Eskimos, who eat them raw or dipped in boiling water or with blubber oil. Höygaard and Rasmussen state that the Angmagssalik Eskimo obtains 50 per cent. of his total vitamin C intake from this source.

SUMMARY.

Employing a modification of the method used by Tillmans, the vitamin C (1-ascorbic acid) content was estimated of a number of common Arctic plants in the region of Revet, Clavering Island, N.E. Greenland. Seasonal variations in the ascorbic acid content of *Honckenya peploides*, *Betula nana*, and *Salix* sp. were also investigated.

The ascorbic acid content of the plants of N.E. Greenland is generally higher than in plants of the same species in S.E. Greenland, and is so high that Europeans there need not suffer from scurvy even without supplies of European foodstuffs and special anti-scorbutic substances.

My thanks are due to Dr. Gilbert-Carter, Cambridge, for kindly identifying my material and to Dr. E. W. McHenry, Department of Physiological Hygiene, University of Toronto, for his valuable criticism. I also bring my thanks to Dr. P. Scholander who made a critical control of the plant identification. Unfortunately, due to war conditions, it has not been possible to submit this paper to the Staff Chief of the laboratory in Oslo before publication.

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ALEXANDER COWAN
1863-1943

OBITUARY NOTICE.

ALEXANDER COWAN.

By the death of Alexander Cowan a link has been severed with a type of botanist which to-day has become all too rare. Schooled at Loretto and at Cambridge, he combined an interest in Nature and the outdoor world in the fullest degree. All aspects of the animal and plant world roused his keenest interest.

It was, however, his love of flowers and ferns that drew forth his affections, and whether in the field or garden he showed an infectious enthusiasm that drew one to his side.

This love of gardens and all they stood for began in his early life. Conceived by his schooling at Loretto, it was while living at Dalhousie Castle that his first contacts with gardens were experienced and where his love for them was nurtured. The art of cultivating garden subjects provided him with a great incentive to acquire plants both rare and common during his travels in Europe. And a visitor to the garden at Valleyfield, Penicuik, would be shown, with modest pride, denizens of alpine meadows of Central Europe which his skill had established with great success.

But both in the garden and in the field it was to the Fern world that he devoted most attention. Not only was he a successful cultivator, and to this the collection at Penicuik and at his country seat at Logan could testify, but he was a member of the British Pteridological Society and attended with great regularity the scenes of its activities. For the unusual or the oddity among the fern groups he had an observant eye, and from every trip into the field he returned with some fern trophy which augmented his collection.

His activities in the Botanical Society of Edinburgh are a noteworthy record. He was elected a Fellow in 1900 and served on the Council for many years. The Society chose him for its President for the Sessions 1937-39, and those who had the privilege of listening to his Presidential Address on his beloved ferns will recall the amazing display of living specimens from his collection which illustrated his lecture.

His botanical enthusiasm had one other outlet—his intimate association with the Alpine Botanical Club. He joined this group of alpine enthusiasts in 1902 and rarely missed the annual excursion

to the mountains. From 1903 to 1924 he acted as secretary and treasurer with an efficiency that was the marked characteristic of any work he undertook.

Other branches of Natural History engaged his attention, and during his early years he took a keen interest in the bird life of his home district.

His outdoor pursuits culminated in later years in a zest for sheep farming. To this he gave much time and study, and on his Pentland Hill farms of Eastside and Logan established a reputation for his stock of the Blackface breed of sheep.

The great work of his life, however, centred in the ancient Royal Burgh of Penicuik. There he laboured in his paper industry, finding time to serve the community in innumerable ways. For over thirty years he was a member of Penicuik Town Council, and for nine years he acted as Provost. He was also a member of the Midlothian County Council for the long period of forty years, and since the outbreak of war had been serving on the Midlothian War Agricultural Executive Committee.

R. M. ADAM.

We are indebted to Messrs. Alex. Cowan & Sons Ltd. for the block of the portrait of Mr. Alexander Cowan.

TRANSACTIONS
OF THE
BOTANICAL SOCIETY OF EDINBURGH

SESSION CIX

PRESIDENTIAL ADDRESS: SOME FACTORS AFFECTING THE NATURAL
REGENERATION OF OAK IN CERTAIN PARTS OF SOUTH-EAST
SCOTLAND. By E. WYLLIE FENTON, M.A., D.Sc.

(Read 15th February 1945.)

Assuming that the war in Europe is nearing the end, it seemed propitious to give as a Presidential Address information on some problems which offer considerable scope to students desirous of prosecuting research in an interesting field of ecology. For this reason, therefore, I present a preliminary and unfinished reconnaissance of some factors affecting the natural regeneration of oak in certain parts of South-East Scotland.

While visiting parts of the unenclosed portion of the New Forest in 1935 one of the most noticeable features was that young oak trees were rare. Yet oak seedlings were plentiful, even on heaths covered by *Calluna vulgaris*. After examining several of the open parts of the New Forest only about a dozen oaks, of ten years or over, were found. The next year in other parts of the South of England this same absence of young oak trees was a common feature with one exception: in Sussex on a small part of waste land near a wood where Whin (*Ulex europaeus*) was plentiful. Growing through the whin bushes were strong, healthy oak trees about 3-4 feet high and also rowans (*Pyrus Aucuparia*) of approximately the same age. This was the only place located where the natural regeneration of oak was successful. This suggested that protection against grazing animals was one reason for this successful regeneration. Next, a search for young oaks was made in the Old Oak Wood in Dalkeith Palace Grounds. It was found that there was a complete absence of young oaks after the first year. In 1938, after discussing this

question with the Head Forester, about $11\frac{1}{2}$ acres of the Old Oak Wood were fenced by the Buccleuch Estates Ltd. against rabbits and hares. No rabbits have been observed, but hares are, or were, frequent at that time. The wood was grazed originally by deer, but during the 1914–1918 War they were killed off and replaced by stock, chiefly sheep. The outbreak of war in 1939 prevented any access to this wood until the latter part of 1943. During the autumn of 1941 many wooded areas in the South-East of Scotland were visited (Fenton (2), 1941), and in 1942 and 1943 further woodland surveys were undertaken as far as time and circumstances permitted (Fenton, 1943). It was hoped that these surveys would yield some information concerning the natural regeneration of oak trees.

The failure of natural regeneration by certain of our forest trees has led to much controversy, and, in the case of certain trees such as oak and beech, to intensive study by Watt (1919, 1923) and Moore (1933, 1936). In Scotland the oak was formerly found in many parts of the country where now it is comparatively rare or absent (Fenton (1), 1941; Tansley, 1939). There are a few isolated places where it seems that conditions should not be unduly adverse for natural regeneration. At Elibank Castle Wood, in spite of quantities of acorns stated to be devoured by wood pigeons, young oak seedlings are by no means uncommon, but young trees are infrequent (Fenton (1), 1941). In certain parts neither burning of heather (*Calluna vulgaris*) nor grazing by farm stock seemed operative, and no evidence could be found of destruction by rabbits. It was hoped to try some plot experiments to test out certain possibilities, but war prevented this scheme coming into operation. Meantime, a rapid survey of Elibank Castle Wood, Haugh Head Wood, Dalkeith Palace Old Oak Wood, and woods in certain other districts was made to check up any significant variations of ground vegetation where young oaks were present or absent. By this means some initial information was obtained as guidance for future lines of work. Unfortunately, transport and other difficulties have made it impossible to extend this investigation. The survey was conducted on similar lines to that used for certain pine woods (Fenton, 1943).

Elibank Castle Wood.—As this rather rapid survey had to be made at infrequent intervals during recent years, many plants which occur at certain times were not very evident. Enough species remained in recognisable form to give a good picture of the vegetation present. September 1942, when the survey was carried out, was a rather dry month and this must be kept in mind when con-

sidering soil conditions at the time of the outline survey. It was not possible to undertake soil investigations. The year 1941-1942 was good for one-year-old oaks at Elibank Castle Wood, the number found being well above the average of previous years. In the following types of vegetation no young oaks were found: (1) *Mercurialis perennis* (D), *Oxalis Acetosella* (S-D), *Viola Riviniana* (C), *Hylocomium splendens*, *Hypnum curpressiforme* and *Mnium hornum*: soil distinctly moist. (2) *Lastrea Filix-mas* (D), *Agrostis* spp. (chiefly *tenuis*), *Festuca ovina* and *Holcus mollis* (C), *Dicranum scoparium* and *Vaccinium Myrtillus* (trace): soil slightly damp. (3) *Luzula maxima* and *Oxalis Acetosella* (Co-D), *Lastrea dilatata* and *L. Filix-mas* (C): soil very damp. (4) *Lastrea Filix-mas* (D), *L. dilatata* (S-D), *Oxalis Acetosella* (F), *Mercurialis perennis*, *Scilla non-scripta*, *Lonicera Periclymenum* and *Holcus mollis* (O), *Luzula pilosa* and *Pteridium aquilinum* (O); birch regenerating: soil damp. (5) *Deschampsia flexuosa* (D), *Agrostis tenuis* (C), *Dicranum scoparium* (L), *Festuca ovina* (O), and *Plagiothecium undulatum*: soil dry on surface. (6) *Polypodium Dryopteris* (D), *Scilla non-scripta* (C), and a little *Lastrea Filix-mas*: soil damp. (7) *Pteridium aquilinum* (D) casting dense shade, little below except a little *Holcus mollis* and *Deschampsia flexuosa*, a few seedling birches: soil rather dry on surface. (8) *Pteridium aquilinum* and *Polypodium Dryopteris* (Co-D), shade rather dense and no ground vegetation: soil rather dry on the surface. (9) *Polypodium Dryopteris* and *Oxalis Acetosella* (Co-D), *Lonicera Periclymenum*, *Holcus mollis*, *Deschampsia flexuosa*, *Stellaria Holostea*, and *Plagiothecium undulatum* (O): soil slightly damp.

Summarising these nine examples, nos. 1, 3, 4, and 6 have damp soil conditions and a rather dense, but not tall vegetation. No. 5, the soil is damp below the surface and there is a continuous grassy covering with moss. No. 7, soil conditions are rather dry on surface and a very dense shade is cast. During autumn, winter, and spring the dead bracken will retain moisture and keep the surface soil very wet. No. 8, the shadow cast is not so dense as no. 7, but is significant. No. 9, some shade effect, and soil not very damp. Generally, nos. 2, 5, 8, and 9 are intermediate as far as soil moisture is concerned.

The ground conditions where young oak trees occurred were distinguished by two main features: (1) Almost without exception there was some litter of leaves, usually oak, and occasionally a little birch. (2) Isolated fronds of bracken were present, but not of strong growth or casting a deep shade. There were a few examples

not strictly conforming to these conditions, but they were all marginal cases. The vegetation types where young oaks occurred were: (1) Where bracken had a high frequency but was not dense or casting a deep shade. The other two species whose frequency ran parallel with bracken were *Oxalis Acetosella* and *Agrostis tenuis*. Almost as frequent were *Holcus mollis* and *Anthoxanthum odoratum*. From a grassland ecology aspect, this vegetation would be regarded as third class of the drier types of soil (Fenton, 1934). This is further emphasised since *Galium saxatile* occurs with a frequency of 29 out of a possible 53. Only in nine cases does this plant occur without bracken being also present. *Hylocomium triquetrum* has a frequency of 20 out of 53. This moss we have generally found associated with rather dry pine woods or birch, but it also occurs among oaks in the New Forest. It is usually replaced by *Plagiothecium undulatum* as shade and moisture increase. *Deschampsia flexuosa* had a frequency of 20/53 and was often locally dominant. (2) Where bracken was not present, or infrequent, the vegetation was of a grassy type, consisting of *Deschampsia flexuosa*, *Oxalis Acetosella*, *Holcus mollis*, *Agrostis tenuis*, *Anthoxanthum odoratum*, and less frequently *Festuca ovina* and *Hylocomium triquetrum*. This vegetation is often associated with dry soil conditions. It has certain resemblance to type no. 5, but is associated with a drier soil. There were three one-year-old oaks found in a vegetation consisting of *Deschampsia flexuosa*, *Oxalis Acetosella*, *Holcus mollis*, *Mercurialis perennis*, *Agrostis* spp., *Luzula maxima*, and *Lastrea Filix-mas*. This is a vegetation occurring on damper soil conditions than the two previous examples. It is probably a border line grouping of oak and these plants. Any further increase in shade seemed to affect adversely successful regeneration. As noted elsewhere the *Lastreas* compete with bracken, and where soil moisture showed a marked increase bracken is rapidly replaced by *Lastrea Filix-mas* and (or) *L. dilatata* (Fenton (2), 1941). Where *Lastreas* become dominant so deep is the shade cast that, with the exception of a few mosses, no other plants generally survive.

It was noted that where birch was regenerating and oaks also occurred, oak was associated with either *Hylocomium triquetrum* or *Hypnum Schreberi* among the mosses, indicating dry rather than wet conditions. Another curious point is that *Mercurialis perennis* and birch rarely occurred together, but in parts where no young oaks were found birch was regenerating on damp soils in a vegetation consisting of *Deschampsia flexuosa*, *Festuca ovina*, *Agrostis tenuis*, *Holcus mollis*, and the moss *Plagiothecium undulatum*. Small birches

were also noted among rather dense bracken where no oaks occurred. It is highly probable that birch would initially outstrip the oak if natural regeneration were to succeed. This might actually be to the ultimate benefit of the oak. It is just possible that some such ground cover might provide the necessary protection and litter during the early and more critical stages of the growth of oak trees. The age groups of oaks are shown in the table. It is evident that in spite of a considerable area of the wood examined, few oaks survive the third year, and there is a heavy mortality after the second year of growth. These observations are not dissimilar to what has been recorded in England by Watt (1919).

Haugh Head Wood.—About two miles west of Elibank Castle Wood lies Haugh Head Wood. This wood had originally been like Elibank Castle Wood, if not once a part of it, but has been planted up, for there are large patches of well-grown beech as well as small numbers of lime, ash, sycamore, and elm; a few larch, spruce, birch, rowan, hawthorn, and a small group of Scots pine. Four Turkish oak (*Quercus cerris*) and also one Spanish chestnut were found. The wood consists of a long narrow strip, in depth varying from two to three hundred yards or a little more at one or two points. It is on a rather steep slope facing north. The elevation is from 500 to 600 feet. There are clear indications of past cutting, mostly oak, for some of the stumps can still be found. In a few places oak trees have arisen from old stumps after felling. Except in the more open parts there is not much grassy covering, but considerable patches of *Lastrea* ferns and *Mercurialis perennis* cover parts of the floor of the wood. Under the beech trees there is no vegetation, and on sloping ground the fallen leaves get blown away leaving the soil bare. In such places there is a gentle erosion of the surface soil. Where there is a grassy vegetation it is thin, the two grasses most plentiful being *Holcus mollis* and *Deschampsia flexuosa*. There are patches of *Mnium* (most *M. hornum*) and in places *Plagiothecium undulatum*. Where *Mercurialis perennis* is present it arrests soil erosion and by its growth holds the litter of dead leaves. In places *Oxalis Acetosella* is present in quantity. The two trees which are regenerating successfully within the wood are ash and, to a lesser extent, sycamore. A few seedling elms were discovered, also four seedling oaks and two beech seedlings. Sheep had broken into the eastern end of the wood, and one result is a colony of stinging nettles. Where the four seedling oaks were found in Haugh Head Wood, ground vegetation consisted of *Deschampsia flexuosa*, *Oxalis Acetosella*, *Luzula pilosa*, *Viola Riviniana*, *Dicranum scoparium*, and some

Plagiothecium undulatum. All seedling trees were suffering from rather serious defoliation by some insect which could not be found. Hence insect damage in the seedling stage may account for part of the heavy mortality of young oaks. There are still small patches where the oak is the principal tree and locally dominant. Even here, however, the ground flora is much poorer than that of Elibank Castle Wood. Rabbit, hare, and sheep grazing probably keep down ground vegetation. There are still *Primula vulgaris*, *Scilla non-scripta*, and in places *Viola Riviniana* and *Veronica montana*. A few plants of *Sececio Jacobaea* and *Epilobium montanum*, *Agrostis tenuis*, *Festuca ovina*, *Anthoxanthum odoratum*, and *Galium saxatile*, were found but were not frequent. There was not much bracken, but in one part an isolated specimen was just beginning to grow in a juvenile form, and must have been propagated by a spore; a rare occurrence in the eastern parts of Scotland.

Dalkeith Palace Old Oak Wood.—Unfortunately, apart from several visits previous to the outbreak of war, access to the fenced part of Dalkeith Wood was not possible till 1943. During this period the old wood was left untouched, except that part used for grazing. By 1943 it showed some interesting changes. Like other oak woods in Scotland it was a rare occurrence to find any young oaks over one year old. Such oaks as did occur were most frequently found under fallen branches, where the twigs of the branches afforded some protection.

In the Autumn of 1943 it was possible to revisit the fenced part and examine the vegetation. The chief item of interest was that young oaks more than one year old were present. The other point of interest was that most of these oaks showed a bushy or shrub-like growth and had not attained any height. Seventy-six young oaks were found, but only twelve of these occurred outside the fenced part of the wood. If the distribution of young oaks is arranged under vegetation types it presents a better picture of the wood. Types dominated by *Agrostis tenuis* were: (a) *Holcus mollis* (S-D), *Pteridium aquilinum* (O): ten oaks 5 years old, two 2 years old, and thirteen 1 year old. (b) *Holcus mollis* and *Teucrium Scorodonia* (O): one oak 5 years old, and six 1 year old. (c) *Anthoxanthum odoratum* and *Rubus fruticosus* (O), and *Pteridium aquilinum*: one oak 2 years old, ten 1 year old. (d) *Festuca ovina* (S-D) and *Holcus mollis*: one oak 3 years old and two 5 years old. *Festuca ovina* dominant: *Agrostis tenuis* (S-D) *Holcus mollis*, *Pteridium aquilinum*, *Galium saxatile*: one oak tree 3 years old. *Holcus mollis* dominant: *Anthoxanthum odoratum* (S-D), *Teucrium Scorodonia*: four oaks

4 years old, one 3 years old, and three 1 year old. *Agrostis tenuis* (pure): two oaks 2 years old. *Ulex europaeus* and *Agrostis tenuis*: one oak 4 years and one oak 1 year old. *Deschampsia flexuosa* (D), *Agrostis tenuis* (S-D), *Potentilla Tormentilla*, *Holcus mollis*, and *Oxalis Acetosella*: two oaks 3 years old. *Deschampsia flexuosa* (pure): fifteen oaks each 1 year old. In the unfenced part of the wood the ground vegetation is generally dominated by *Holcus mollis* and *Agrostis* (chiefly *A. tenuis*). It is rather a dry type with *Pteridium aquilinum* lightly scattered over the ground with some dense patches.

In the fenced area the vegetation is becoming very dense in parts. There is much *Dactylis glomerata* and *Arrhenatherum avenaceum*, and this vegetation is tending to spread. *Oxalis Acetosella* is still present in parts. Moisture at ground level is much higher than formerly and suggests that this favours not only germination but survival of young oaks.

Environs of Elibank Castle Wood.—In July–August 1943 a survey was made of certain parts lying outside the confines of Elibank Castle Wood, to obtain further information on the natural regeneration of oak. Part of the hillside above was also examined for comparison with that part lying within the wall. The elevation lies between 400 and 500 feet. The first part examined was at the extreme west, and covered by a grassy vegetation, following the removal of trees some time ago, perhaps twenty-five years previously. There were patches of bracken and *Lastrea*, but *Deschampsia flexuosa* (D), *Festuca ovina* (O), *Agrostis tenuis*, and *Anthoxanthum odoratum* constituted the grassy vegetation with occasional patches of *Holcus mollis*. *Galium saxatile* was common, while *Potentilla Tormentilla*, *Viola Riviniana*, *Lathyrus montana* were scattered over most of the area with a small amount of *Rubus Idaeus* and *Scilla non-scripta*. Also present were *Oxalis Acetosella*, *Anemone nemorosa*, *Lonicera Periclymenum*, *Calluna vulgaris*, *Hypericum pulchrum*, *Lotus corniculatus*, *Scabiosa succisa*, *Veronica montana*, as well as small patches of *Urtica dioica* and one of *Digitalis purpurea*, *Empetrum nigrum*, and *Erica cinerea*. The highest part near the wall was covered by a dense growth of bracken. Generally, this is no. 5 type of vegetation and no oaks were found.

On the hillside above the wall surrounding the wood lay a typical *Calluna* area. Burning had occurred in the past and as a result there was a dense patch of bracken next the wall, extending for some distance up the hill. Immediately above this was a patch of larch from 10–20 feet high. Below, the vegetation was *Calluna*

vulgaris and a few scattered bracken fronds, the *Calluna* was long-stemmed, deep, and had not been burned for many years. Within this patch of larch two young oak trees were found which had arisen by natural regeneration. The oaks had long stems, following the line of heather stems, with a good tuft of leaves at the top. The stems were about 18 inches long. Comparing these with oak of a similar size elsewhere, they were about 5 years old.

Immediately to the east of this Larch copse lies a few scree-like bare parts, mostly loose stones, although the slope is not steep. Here *Polypodium Dryopteris* is present in patches, a little *Prunus spinosa*, one hawthorn bush, and a few thin straggling bushes of *Rosa canina*. From these indications and the mosses present, there is little doubt that formerly this part had been wooded, and that most of these plants are virtually remnants of a relict flora. Birch and *Pyrus Aucuparia* with *Salix caprea* and one Scots pine are the only evidence of natural regeneration, apart from the two oak trees and some older shrubby oaks occurring farther east, recorded some years ago (Fenton (1), 1941). It is possible that a more detailed search might reveal a few prostrate shrub-like oak trees in outlying parts of the hill.

Previously young growths, or what appeared to be young growths, arising at or near the base of a few oak-tree trunks were not recorded. This was because they were considered to be arising from the basal part of the tree. It was not thought advisable to proceed pulling up these to decide their origin. However, a few rather suspicious growths were noted and dug up, and it was found that some of these were actually young oaks, quite independent of the parent tree. Without sacrificing such growths it is quite impossible to even guess the proportion of these which may be young oak trees. The inclusion of these would be quite insufficient, however, to achieve successful natural regeneration.

In the past we have found a considerable amount of dead acorns lying on or just below the soil surface and its vegetation. Some of these acorns had been nibbled, others seemed to have been attacked by insects and some by fungi. Many acorns found were dead and decayed with no evident sign of any disease or damage. This suggests that there is not a high germination rate of acorns. When to this fact is added the high mortality of young oaks, it is clear that under present conditions the percentage of survival must be very low.

Environs of Haugh Head Wood.—By far the most interesting find was a small fragment of woodland lying at 700 feet elevation on

the upper side of the extreme western part of Haugh Head Wood. Here a small patch of stunted, twisted and gnarled oaks was found mixed with some birch. This is evidently all that remains of an old semi-natural or natural wood. This part lies open on the hillside above the protecting wall. It is open to grazing by sheep and any other animal on the hillside, which was a typical *Calluna* heath. There is a thin vegetation cover under the oaks consisting of *Deschampsia flexuosa*, *Agrostis tenuis*, *Holcus mollis* (O), small quantities of *Calluna vulgaris*, *Erica cinerea*, *Vaccinium Myrtillus*, *Oxalis Acetosella*, *Veronica montana*, *Festuca ovina*, *Hypnum Schreberi*, *Dicranum scoparium*, *Hylocomium triquetrum*, *Pteridium aquilinum*, and *Cladonia sylvatica*. There were no young oak plants to be found beneath these trees (*Quercus sessiliflora*). It was noted, particularly in one tree, that some of the roots were giving off a vigorous series of shoots, rather after the fashion of elm trees. This continued for more than a yard from the trunk of one tree. A few other examples were found, but not quite so pronounced as the tree just cited. This also occurred to a lesser extent within Haugh Head Wood proper, where oak stems of small size were found growing close together in line, having obviously arisen in this way. It would appear that certain oaks may in this way achieve vegetative propagation. When to this is added the oaks which arise from the basal stump of felled trees, it is evident that the oak may still linger on in spite of the failure of natural regeneration from acorns.

On the north-eastern fringe of this patch of oak trees are young birch trees which have arisen by natural regeneration. Below occurred *Calluna vulgaris* (O), a little *Erica cinerea*, *Vaccinium Myrtillus*, *Deschampsia flexuosa* (O), *Hypericum pulchrum* (O), *Potentilla Tormentilla* (O), with a few small patches of *Leucobryum glaucum*. There was some litter of oak and birch leaves. In the vegetation, where *Calluna vulgaris* was at least a foot high, a few young oak trees were found which had risen by natural regeneration. One was 4 years; two 3 years; and four 1 year old. Hence under cover of the birch and heather with the litter of leaves oak can regenerate, but this is only where there is no heather burning and where there is ground protection against grazing. As soon as an oak or rowan (*Pyrus Aucuparia*) arises above the level of the heather it is grazed, presumably by sheep. The only rowans found of any height and ungrazed were in another place, where heather had reached a height of 3 feet and with this protection two young rowan trees were flourishing. In almost every other place, rowans of every age had all been topped. The 4-year old and the two 3-year

old oaks had been damaged at the top by grazing. Evidently sheep had nibbled at the tips of the heather, and in doing so the oaks had suffered. Two young beech trees were also noted in similar vegetation.

TABLE SHOWING YOUNG OAKS UNDER AGE GROUPS.

Age in Years.	Dalkeith.					Elibank.		Haugh Head.		Peebles.
	1943.		1944.			1943.	1944.	1943.	1944.	1944.
	F.	U.	F.N.	F.	U.					N.
1	36	12	1	36	85	15	23	4	21	0
2	5	0	1	15	11	22	40	0	2	2
3	5	0	1	6	0	9	29	0	1	3
4	5	0	6	8	0	0	3	0	0	6
5 +	13	0	12	25	0	3	4	0	0	3

F.=fenced against grazing.

U.=unfenced.

N.=no tree cover.

5 +=5 years and over.

Inadequate as the figures may be, they do show that grazing is certainly a factor of major importance in preventing natural regeneration of oak in Dalkeith Old Oak Wood. This is further emphasised in 1944, where the area formerly grazed had 85 one-year-old and, for the first time, 11 two-year-old oak trees. The reason for this large increase in the first-year oaks and the survival of 11 oaks into the second year was that during 1944, owing to military exercises, there was very light or, more probably, no grazing of any kind. There were no traces of any grazing during the times that reconnaissance was made. The increase in the figures for 1944, both for Dalkeith and Elibank, is due to a more intensive and detailed reconnaissance. The ages of the trees are approximate, as only a very few were cut to test the estimations of age judged by external appearance. For this reason some of the ages may need reviewing, but the figures are substantially correct. As there was no evidence of grazing at Elibank Wood, any difference in numbers is probably due to the more intensive survey of 1944. Haugh Head Wood, like Roslin Glen, has been so much affected by human interference, both direct and indirect, that it would not be safe to venture any comparisons. Another factor which should be mentioned is rainfall. During the late summer and autumn of 1944 rainfall was unusually heavy and this did affect ground vegetation.

The density of ground cover increased in every wood, although this was becoming evident even before 1944, but until then it was a very slow change. This doubtless was due to these areas being left undisturbed.

The question of ground vegetation is both interesting and important. In Dalkeith in 1944 a small part was examined for the first time. It lay outside the wood proper, but within the area fenced off. It is under the letters F.N. for Dalkeith 1944. The interest of this small corner of the fenced part is that with no tree cover acorns have reached it and commenced growth from the date of fencing, as the figures indicate. With the passage of time and no tree cover, the grassy vegetation has become both tall and dense, in several parts dominated by *Dactylis glomerata* and *Arrhenatherum avenaceum*. So dense have these two grasses become that it would seem virtually impossible for natural regeneration of oak to succeed. The figures, such as they are, support this view. Moreover, in 1944 no seedling trees occurred where these two grasses had reached a certain height or density of ground cover. Further evidence of this is also found in the Peebles figures in the Table. The history of this part is not dissimilar to Dalkeith. The part concerned has not been grazed since the outbreak of war. The ground vegetation is grassy and generally dominated by *Holcus mollis*, with some *Festuca ovina*, *Agrostis vulgaris*, *Anthoxanthum odoratum*, and a few tufts of *Deschampsia caespitosa*. Mosses present were *Hypnum Schreberi*, *Hylocomium splendens*, a little *Brachythecium purum*, and patches of the lichen *Peltigera canina*. Other plants present in the immediate vicinity were *Rosa canina*, *Crataegus monogyna*, *Centaurea nigra*, *Luzula pilosa*, *Rumex Acetosa*, and *Hypericum humifusum*. Litter of tree leaves was scanty, but there was a good deposit of dead grass leaves and stems. In fact the condition of this grassy patch was what a farmer would call "foggy", or in other words grassland with, on the surface of the soil, a deposit of dead, undecayed grass leaves and stems. A total of fourteen young oaks were found after a search. The ages of these are given as approximate since none were sacrificed to determine the age by a cross-section of the stem. Three were about 5 years old or older, bushy in appearance and about 2 feet high; one about 4 to 5 years old; five were about 4 years old; three were 3 years old; and two were 2 years old. In every case the original apical bud or leader of the tree had died, and in several cases this had occurred regularly for several years in succession. The bushy growth is due to side buds sending out shoots. In a few trees the present growth had started right back on a former

main stem almost at ground level. It was evident that any growth showing above grass level had occurred within the last five years.

Even outside the woods considered and their environs, there has been noted natural regeneration of other trees than oak. For example, on a part of the old Drove Road from Peebles to the Traquair Valley in 1944 there was found spruce, birch, and a few seedling beech trees. Similar examples could be quoted, and the reason is the drastic reduction of the rabbit population and better fencing preventing sheep or cattle breaking out of fields or enclosures.

From the vegetation types where natural regeneration of the oak does not occur in Elibank Castle Wood, it is evident that in nos. 1, 2, 4, 7, and 8 shade is a limiting factor. In no. 9 shade is also of some significance. Nos. 3 and 6 are not quite so evident but shade is still of some importance. Nos. 1 and 3 have soils which at the time of investigation were wet, while nos. 5, 7, and 8 were dry. It may be that excessive moisture, or too little moisture, are unfavourable for natural regeneration. Hence the exact nature of the vegetation type may not be so important in itself if certain other factors such as shade and excessive moisture, or lack of moisture, outweigh vegetational variation. In Elibank Wood, where oak is tending to regenerate naturally, the two outstanding factors were not too dense shade and a certain amount of litter from fallen leaves. Generally speaking the two types were equivalent to a third class grassland of the drier type (Fenton, 1934), where bracken is sparse or absent. This naturally raises the question as to why natural regeneration did not occur in type no. 5 in Elibank Castle Wood. The reasons probably lie in the fact that first there was no litter of leaves, and second that the soil in that type was dry. Another point of importance is the small extent of no. 5 type of vegetation and that the chances of many acorns reaching this type were not numerous.

Turning next to Dalkeith, the vegetation types there are all grassy. But there again it must be remembered, as judged by the Peebles vegetation, "litter" of grass leaves may replace litter of deciduous trees. The outstanding feature of the Dalkeith Wood is that over a long period the wood was utilised for grazing. This naturally destroyed any shrub layer and produces a grassy floor covering. With the passing of the grazing factor Dalkeith is beginning to show tendencies of developing an intermediate layer of vegetation, for bracken is now spreading as well as *Rubus fruticosus* and *Rubus Idaeus*, holly, birch, and hazel. There is also a danger of surface drought in many of the more open spaces of Dalkeith Wood

where the oak trees are widely scattered. Not only in summer but at times even in late autumn drought is by no means unusual and would not be very favourable for natural regeneration. This drying up of surface moisture has been noted in places in the Tweed Valley and occasionally may occur even in spring. It would appear that tree (or shrub) cover is important in preventing this drying out process.

This drought affect may partially explain why in places acorns may be found just at or below the surface of the ground with no apparent injury by animals (including insects) or fungi. They seem quite sound but have failed to germinate, and still deeper they also occur slowly decaying. At times there occurred a faulty germination, where the development is abnormal, often due to failure of root growth. This may be due to some kind of external injury, but no satisfactory evidence of this could be found. It would appear that there is an appreciable loss due to this failure to germinate successfully. Another aspect of this may at times be noted, where young oaks do not occur in spite of conditions which seem quite favourable. Yet ash, sycamore, and birch regenerate naturally and successfully when oak fails.

The areas examined outside Elibank and Haugh Head Woods showed clearly the importance not only of the grazing factor but also of fire. Where a heathy vegetation is regularly or periodically burned natural regeneration is impossible. Another factor of importance is some protection in the early stages of natural regeneration. Where heather (*Calluna vulgaris*) was long and had not been burned young oaks were by no means rare. Although the total number of young oaks found was not large, the area of unburned heather was very restricted. With a larger extent of unburned heather natural regeneration might have been adequate. The successful natural regeneration of oak under conifers is particularly interesting. This method was used long ago in certain parts of Scotland (Donaldson (1), 1794) and is still used in certain parts of England, where it has been found useful to protect young oaks against frost and cold spring winds. The question naturally arises as to whether, or to what extent, the oak in its younger stages of growth is a light demander. The oak tree is commonly regarded as a light demander. This is a matter that requires further investigation.

No less than twelve oak trees were located in the Tweed Valley which had arisen from the cut stools of old oaks. The regular cutting of oaks in the past was a general practice to obtain the bark,

which was necessary for tanning. There are frequent records of this in the *First and Second Statistical Accounts of Scotland* (1791, 1826). Many of our present oak trees which still survive in Scotland owe their origin to this coppicing system. It is also recorded in the *Statistical Accounts of Scotland* that failure to fence against grazing animals led to the exterminating of many of these coppiced woods. It is stated that where fencing is used the woods recover, but where not done they are killed by grazing. This is probably one of the earliest records of the importance of the grazing factor. This is also noted by Donaldson (2) (1794), who records a fine oak wood near Elgin. The growth of new trees from old stools can be seen after ash and sycamore are cut. In many parts, however, where coniferous and non-coniferous trees grow side by side, the young shoots arising from the stools of cut deciduous trees are frequently completely ringed and killed by rabbits. We have noted this in many woods felled in recent years.

Damage caused by animals, excluding farm animals and rabbits, may be severe. So far as we have been able to gather evidence, there was some evidence of insect damage at Haugh Head Wood. It would require several years of continuous observations to assess the damage, if significant, due to this cause. Although mildew is often frequent on the sappy growth of oak shoots from old stools, no attack in young oaks has so far been noted. Damage by mice and voles doubtless occurs, but no reliable information is yet available. The war has made it impossible to lay out a series of plots to investigate this question. They certainly did damage in the past as recorded by Haddington (1761), nearly two centuries ago.

Perhaps one of the worst problems which greatly reduce natural regeneration is the so-called non-pathogenic die-back disease of young oaks. This die-back is well known in most parts of England, wherever natural regeneration tends to occur. Several suggestions have been made as to the cause: such as impaired ripening of, and drought affecting, the apical bud. Until the problem has been thoroughly investigated it is better not to consider too many theoretical possibilities. A recent suggestion is that it is due to mildew attacking the apical bud and overwintering there. That mildew can cause serious and fatal damage is well known. Even full-grown oak trees may suffer (Day, 1927). In nurseries severe losses may occur (Woodward, Waldie and Steven, 1929). As work is proceeding at the present time on certain mildews (Weston and Taylor, 1945), it may be that this will ultimately shed fresh light on this problem. This non-pathogenic die-back occurs both in Roslin

Glen and in the Tweed Valley. The examples of die-back noted were all recorded in summer, and there was then no sign of any visible mildew present on the young oaks or on older trees.

Past writers (Aiton, 1811; *Statistical Accounts of Scotland*, 1791, 1826) frequently refer to the vast extent of oak forests in Scotland. For example Aiton (1811) states that Selkirk Forest stretched from Selkirk to Ayr, Strathaven, and Mauchline. Even after the Reformation he quotes places where remnants of this forest still survived. The question naturally arises, why did this forest so quickly disappear and how natural regeneration did not make good at least part of the loss? Aiton (1811) states that in places remnants might have survived if they had been protected or fenced against grazing. Had this been done perhaps natural regeneration might have occurred. Another possibility arises, however, which may be and, doubtless, still is effective. Salisbury (1922) points out that extensive clear felling tends to lead to soil erosion and leaching. This makes the soil more acid and retards or may prevent natural regeneration of oak. This same process is also referred to by Hessleman (1916) who pointed out that, in Scandinavia, spruce trees had failed to regenerate naturally as they formerly did owing to this increase of soil acidity caused by the removal of the tree cover. It is by no means impossible that following devastation of these oak forests by man, increasing acidity of surface soil and no annual drop of acorns made natural regeneration impossible.

Turning next to a consideration of conditions in England, a good but brief summary of the present conditions is given by Tansley (1939). Watt (1919), however, still remains the outstanding source of information, although Moore (1933, 1936) has tested out some of Watt's findings in the south-west part of England. Watt deals with every aspect of the situation as it occurs in England, and it is interesting to note how his findings are largely in agreement with present known conditions in the south-east of Scotland. Watt (1919) shows that there is a very heavy mortality of acorns if there is a moisture loss of about 20 per cent. If this exceeds 27 per cent. then the acorn fails to recover moisture and dies. If the loss is not so great the acorn may make good the loss and survive. Obviously the surface vegetation and certain other conditions play a very important part in determining the survival chances of acorns when they fall to the ground. The great advantage of litter in both hiding the acorns and affording protection against undue loss of moisture is stressed. This is very evident in Elibank Castle Wood.

Tall grass may prevent acorns reaching the soil and thus getting dried out. The evidence of this at Dalkeith Old Wood is not entirely conclusive. So far as information is available, the shading effect seems more important, for young oaks were previously found in patches of tall *Dactylis glomerata* and *Arrhenatherum avenaceum*. *Deschampsia flexuosa* and *Agrostis tenuis* are recorded by Watt as not good for successful germination. At Elibank Castle Wood this seems generally true, but is not so marked for *Deschampsia flexuosa* in Dalkeith Old Oak Wood. *Holcus mollis* and litter are recorded by Watt as good and the evidence for Elibank Castle Wood bears this out, but for Dalkeith Old Oak Wood this feature is not so evident. It is probably a moisture problem, as Dalkeith Old Oak Wood is in many parts more open and tends in summer to be much drier, while the grazing factor must be kept in mind.

It was also shown in England that protection against grazing animals had a very important influence on the survival of young oak trees. This was true both for fenced areas as well as where holly, sloe, and hawthorn gave natural protection. Young (1935) also refers to the importance of enclosure against grazing in the New Forest. Most interesting is the fact that at Petworth, Watt (1919) found young oaks flourishing in clumps of *Ulex europaeus*, as we also noted in Sussex in 1936. Young oaks also occur with whin (*Ulex europaeus*) in the fenced part of Dalkeith Old Oak Wood. Recently we found a small patch of whin on a roadside just south of Gala-shiels. There were eight young oaks, 3 years or more in age, in or near a clump of whin bushes. Farther along the roadside only two other young oaks could be found although various vegetation types were present. There were no traces of grazing by rabbits. This raises the question as to whether the successful association of oak regeneration with whin has some deeper significance than merely protection against grazing animals. A series of experimental plots to investigate this question might provide some very interesting and valuable information. At Petworth, where rabbits were treated as vermin, there was no lack of young oaks. In England there is a heavy loss by mice and voles, both above and below ground level. This is largely due to the constant destruction and suppression of the natural enemies of these pests. So far, we have insufficient information for Scotland to make any statement regarding losses due to these animals. Only careful plot work, and close and continuous observations will supply the necessary information. It is interesting that Moore (1936) concluded from plot work in South-Western England that rabbits

and not field mice were the chief cause of the failure of oaks to regenerate naturally.

The frequency of *Holcus mollis* on the floor of woods is rather striking, for it is not confined to deciduous or even mixed woods but may also be found in coniferous woods of the open type. This grass is often associated with rather shady conditions (Jeffreys, 1917) and is often associated with oak woods. Its frequent presence in the Tweed Valley, even in rather open coniferous woods (Fenton, 1943), strongly suggests that conifers have been planted on potential oak or deciduous tree soil. In places there is evidence to support this view. Perhaps the cult of the coniferous wood may be partly responsible for the almost complete disappearance of the deciduous wood in Scotland, and in places the planting of conifers in rather unsuitable soil conditions (Fenton, 1943).

In England artificial regeneration of oak has already started, at least on an experimental scale, and affords some very interesting information (Guillebaud, 1930). It would provide some very interesting facts and figures if similar work was undertaken in Scotland, for it might provide some of the answers to problems affecting natural regeneration.

After discussing certain aspects of the natural regeneration of oak, it is necessary to refer to types of oak trees which occur in the districts considered. Dr. E. W. Jones of the Imperial Forestry Institute has been very helpful and has identified large numbers of samples drawn from various parts of the South-East of Scotland. The oak samples from the Old Oak Wood in Dalkeith Palace Grounds were, with one exception, *Quercus pedunculata* as assessed by a very large number of samples. There are some which show considerable variation. Near Penicuik the trees are pedunculate with few exceptions. Near Haystoun (Peebles) pedunculate oaks are five to every one of sessile, although some of the pedunculate types seem hybrid. At Neidpath (Peebles) pedunculate oaks predominate with pedunculate variations (very near *pedunculata*) and only two sessile types. Near Manor Sware (Peebles) one-third is pedunculate and the remainder pedunculate type with intermediate characters. Between Peebles and Traquair the pedunculate type is predominant with variations and just a few sessile types. At Elibank Castle Wood there is no pure typical *pedunculata*. Types of varying degrees between pedunculate and sessile are plentiful and just a few which can be termed sessile. Generally the majority are nearer the sessile type. Near Holylee, opposite Elibank Castle Wood on the north side of the Tweed, the oaks are mostly peduncu-

late, or of that type, very few are sessile, but there are variations. In Roslin Glen the sessile type is complete, although a few variations were found.

Turning next to the Selkirk, Clovenfords, and Galashiels district the following figures were obtained from samples drawn: Selkirk-Raelees Wood, 14 pedunculate, 9 intermediate, and 1 sessile; Raelees Wood-Clovenfords, 12 pedunculate, 4 intermediate, and 4 sessile; Clovenfords-Galashiels, 6 pedunculate, 4 intermediate, and 3 sessile; Galashiels-Raelees Wood, 15 pedunculate, 6 intermediate, and 6 sessile. The intermediate types were very variable, some were very near either the pedunculate or the sessile type.

It has been generally assumed that the pedunculate and sessile oaks hybridise and that these curious and often varied intermediate types were hybrids. A recent view is that many of these variations are not hybrids but merely divergent forms either from pedunculate or sessile oak. Poskin (1934) in his monograph on oaks is doubtful concerning the frequency of hybrids. Dengler (1943), however, puts this to the test by cross pollinating the two oaks and assessed the probable result under natural conditions at 2 per cent. success. In view of this it will be necessary to reorientate our views regarding these many "intermediate" forms and to prosecute further research into this very fascinating but difficult question. This leads naturally to the question of the distribution of pedunculate and sessile oaks. It has generally been accepted and assumed that the pedunculate is found on clay, heavy, and the more fertile soils of the lowlands and the foot of valleys. The sessile oak, on the other hand, has been associated with steep slopes, thin, poor, and siliceous soils. Generally there is much truth in this, but there are many exceptions (Tansley, 1939). It may be that the extraordinary variations from the central type partly explain this rather puzzling situation. Evidently much work remains to be done before any definite conclusion can be reached.

There are a few points which are worth mentioning as they may prove useful to those investigating some of these problems. Identifying of seedling oaks is most easily done in spring or early summer when the young leaves have a yellow or pale green colour frequently with a tint of red. It is very easy to distinguish the oaks from the rest of the ground vegetation when these colours are present. If the reconnaissance is done later it is extremely difficult to pick out seedling oaks from the rest of the vegetation and many oaks may be missed. To assess the age of certain young oaks it is necessary to sacrifice several by cutting across the stem to make certain of the

age. Growth is so variable in some instances that unless this is done it is almost impossible to assess the age with any degree of accuracy. To follow the history and progress of young oaks it is necessary to mark them and also put a tally or mark in the ground near them. Only by such means can one follow from year to year what is happening to trees of varying ages in the early stages of growth. Plots will also be necessary, whether these are specially selected or a small area completely divided up into a series of plots. By such means different types of vegetation can be considered and useful information gained. Another point of some importance is to examine the base of all young oaks at ground level, particularly where the ground vegetation is dense. It is not unusual to find that what at first appears to be a seedling oak is a shoot arising from an older stem near ground level. Hence what appears to be a one-year-old may be three or perhaps five years old.

Much work has been done on woodland ecology in England. So far, we have not been so fortunate in Scotland. From this outline of the position of the oak it is evident there is a wide field for research which Scottish students should not neglect.

SUPPLEMENTARY NOTE.

Felling has been in progress during the present year (1945) at both Elibank Castle Wood and at Haugh Head Wood. A part of both has been clear felled and there has also been selective felling, with considerable disturbance of ground vegetation with consequent interference with natural regeneration of oak.

In Dalkeith Old Oak Wood—unfenced part—cattle and sheep grazing has occurred (1945). This has in most parts greatly modified ground vegetation from its 1944 condition. After a very careful survey, a total of 58 young oaks were located. At least two-thirds of these were one year old, leaving only 38 survivors of the 112 originally noted in 1944. All these oaks were under fallen branches or in dense growth where no grazing had occurred.

Two young oaks were found (Dalkeith) in September 1945 with some mildew on the leaves but were growing in very shaded situations. In the enclosed part a few oaks of 5 years showed traces of mildew on some of the leaves, but these were exceptions. It is therefore evident that mildew is not common on young oaks at Dalkeith, though it is found on some of the very old trees.

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NOTES ON LICHENS IN THE HERBARIUM OF THE ROYAL
BOTANIC GARDEN, EDINBURGH. IV. By W. WATSON, D.Sc.

(Read 17th May 1945.)

Since the publication of my Lichen Notes in these *Transactions* (1942, 183–208) some unnamed specimens, collected by the late C. V. B. Marquand, have been added to the Herbarium and these were sent to me by Mr. Young for identification. Mr. Marquand was not a lichenologist, but sometimes collected lichens and, as his excursions often extended into regions little frequented by lichenologists, it is not surprising that some of his plants are new for the counties where they were obtained. A complete list of the determinations is not necessary as many of the common plants had already been recorded for the counties in which he had obtained them, but the most important and all the new vice-county records are given.

A number of plants which have been sent by other collectors and determined or confirmed by me are included in the list when they are new records for the botanical vice-counties of Scotland. A few which had been collected by Lauder Lindsay or other collectors of the last century and had been overlooked in former notes are included. Mr. Young sent me his own gatherings for determination and any new Scottish v.c. records are included. Other new v.c. records of Scottish plants sent by R. Burn of Oxford, F. A. Sowter of Leicester, E. C. Wallace of Sutton, and Ursula Duncan of Arbroath are included. The greatest number of records were due to the successful activity of Miss Duncan. Not only has she explored her own county of Angus, but during her war work was able to obtain, and in most cases correctly name, many rare lichens from the Grampians and other mountain ranges. Her additions are so many that it seemed unnecessary to occupy space to indicate them, so that all those without indication of any collector are due to her activity. All the lichens mentioned have been seen by me; the few for which I am entirely responsible are indicated by W. W. The names of other collectors are sometimes indicated by initials or by an abbreviation of the surname.

The numbers refer to the botanical vice-counties in which the lichens were found, and the addition of an asterisk indicates that the plant was not known to have been recorded for the vice-county.

LIST OF LICHENS.

- Parmelia delisei* (Dub.) Nyl. Norman Law (85*) W. Young. Glen Brittle, Skye (104*).
- P. pubescens* var. *reticulata* (Wulf.) A. L. Sm. Near Invermoriston (96*).
- P. corniculata* (Light.) A. L. Sm. Slochd Mor, Ben Avon (94*) E. C. W.
- Hypogymnia physodes* form *labrosa* (Ach.) Wats. Falkland (85*) W. Young; var. *tubulosa* (Schaer.) Wats. Ullapool (105*). The form which Bitter has elevated to the rank of a species as *Parmelia farinacea* has been sent to me from Woodhall (77*) R. Burn, and on larch from Braemar (92*).
- H. vittata* (Ach.) Gasilien. Carr Bridge (96*) and near Clune Inn (97*). The thalline margins are dark, innovations occur and perforations are present.
- Platysma lacunosum* (Ach.) Nyl. (*Cetraria norvegica* DR.). Near Inverfarigaig (96*).
- Lecanora albescens* var. *dispersa* (Pers.) Arn. Ethie (90*) and Ullapool (105*).
- L. hageni* var. *marina* (Wahl.) Th. Fr. Lentram, near Inverness (96*).
- L. chlarona* (Ach.) Nyl. Black Isle (106*).
- L. intumescens* (Reb.) Krb. Ullapool (105*).
- L. gangaleoides* Nyl. Braidowne, Clova (90*). Laig Bay, Eigg (104*) Marq.
- L. cenisia* var. *atrynea* (Ach.) Harm. Arbroath (90*).
- L. carpinea* (L.) Wain. Arbroath (90*) and Black Isle (106*).
- L. sambuci* Nyl. Dochgarroch (96*).
- L. conizaeoides* Cromb. Woodhall (77*) R. Burn.
- L. sulphurea* Ach. Near Redhead (90*).
- L. intricata* Ach. Near Bonar Bridge (108*).
- L. polytropa* (Ehrh.) Schaer. On rocks, Applecross (105*) Marq.; form *subglobosa* Cromb. Clockstrigg (90*); f. *alpigena* Leight. Glen Phee (90*); f. *illusoria* (Ach.) Harm. Tarbert (110*) Marq.
- L. epanora* Ach. Near Pitlochry on S. side of river (89*). Also Glen Beag, W. Young.
- L. symmicta* var. *sepincola* (Ach.) Nyl. Invermoriston (90*).
- L. orosthea* Ach. Near Redhead (90*). Strathpeffer (106*).
- Aspicilia laevata* f. *pallidior* Magn. Glen Nevis (97*) W. W.
- A. superiuscula* (Nyl.) Hue. Miss Duncan got some so-named material from Loch-na-Gat (88), the locality where Crombie originally collected the plant. It seems to be correctly named,

but there are slight differences from Crombie's description. He gave the paraphyses as discrete and spores as $10-14 \times 7-8 \mu$, whereas in Miss Duncan's gathering the paraphyses are not really discrete and the spores are $10-11 \times 5-6 \mu$. A. L. Smith also qualifies Crombie's description, giving the paraphyses as subdiscrete and the spores as usually about $10 \times 6 \mu$.

Ochrolechia pallescens (L.) Mass. Loch Arkaig (97*) Marq.

Biatora quernei (Dicks.) Fr. Blair Atholl (89*).

B. coarctata var. *elachista* (Ach.) Th. Fr. Near Arbroath (90*).

This agrees with form *variolora* Flot.

B. granulosa Mass. Newarkhall (77*) R. Burn.

B. tenebricosa Ach. Carr Bridge (96*). Vainio gives this under *Lecidea erythrophaea* Flk. with three forms, *tenebricosa* with a brown disc to the apothecium, *rufescens* with a red disc, and *testacea* with a paler disc. All these different colours were present in the apothecia of the Carr Bridge specimen which certainly consisted of the same kind of plant.

B. ochrococca Nyl. Near Tomich, Strathglass (96*).

B. fuscorubens Nyl. Laig Bay, Eigg (104*).

Lecidea parasema Ach. Black Isle (106*); form *conspurcatorosorediosa* Harm. Inverarity (90*); var. *flavens* Nyl. Glen Moriston (96*).

L. assimilis Th. Fr. W. side of Laig Bay, Eigg (104*) Marq.

L. cyathoides Ach. (= *L. rivulosa* Ach.). Invermoriston (96*), and near Bonar Bridge (108*); var. *infusata* (Magn.) comb. nov. Tarbert (110*) Marq.

L. kochiana Ach. Near Ethie Haven (90*) and near Bonar Bridge (108*).

L. contenebricans Nyl. Leith Hill (17*) Marq.

L. mesotropiza Nyl. Invermoriston (96*).

L. lapicida Ach. Near Bonar Bridge (108*). Tarbert (110*) Marq.

L. alpestris var. *brachyspora* Lamb. Ben Doran (98*).

L. lithophila f. *ochracea* (Ach.) Nyl. Glen Fee (90*) W. Young.

L. lithophiliza Nyl. Glen Doll (90*) W. Young. The dark line below the white hypothecium is well shown and other characters are agreeable except that the apothecia are larger and more elevated than usual.

L. consentiens Nyl. Craig Rennet, Glen Dole, Clova (90*). The thallus has no coloration with calcium hypochlorite, the hymenium is high (to 240μ) and the spores are large (to $30 \times 17 \mu$). Cephalodia are present and contain brownish-green or bluish

algae. Dr. Lamb places *L. consentiens* with *L. pelobotryon* and considers that our British specimens of *L. panaeola* belong to the same species.

L. mersata Stirt. Suanaral, Lewis (110*) Marq.

L. macula Tayl. On boulders, Braidownie, Clova (90*). New to Scotland. The specimen agrees with the description in A. L. Smith's British Lichens, and the following additional notes are given. Epithecium variable from brown to greenish or bluish (with nitric acid somewhat purplish), hymenium low (if one neglects the upper pale portion of the hypothecium it is less than 40μ), asci small, about $20 \times 9\mu$.

L. silacea Ach. Near Pitlochry (88*).

L. fuscoatra var. *grisella* (Flk.) Nyl. Near Lundie Crags (90*); var. *mosigii* (Ach.) Nyl. Moulin Moor, Pitlochry (89*).

L. dicksonii Ach. Near Tarbert (110*) Marq.

L. contortula Stirt. Glen Nevis (97*) W. Young.

L. percontigua Nyl. Applecross Forest (105*), and Tarbert (110) Marq. *L. corollidia* Stirt., which has priority, probably refers to the same plant.

L. albocoerulescens (Wulf.) Ach. Rum (104) and near Tarbert (110) Marq.

L. flavocoerulescens (Horn.) Ach. Dalwhinnie (96*) Linds.; Cuillin, Skye (104*) Marq.

L. promiscens Nyl. Cambus o' May (92*). This sec. A. L. Smith's Monograph includes *L. inops*. Th. Fr. If these are kept as separate species, Miss Duncan's specimen is better under *L. inops*, as the apices of the paraphyses are bluish and the spores smaller than in typical *promiscens*.

L. cinerascens (With.) A. L. Sm. *L. speirea* Ach. Glen Feshie (96*) W. Smith, leg. 1889.

L. crustulata form *ferruginea* Kremp. Quirang (104*) leg. Lindsay.

L. dealbatula Nyl. Kinnoul Hill (89*) Lindsay.

L. furvella Nyl. Above Invermoriston (96*).

Pertusaria lactea (L.) Nyl. L. Brittle, Skye (104*) Marq.

P. leptospora Nitsch. Near Inverfarigaig (96). New to Scotland.

P. dealbescens Erichs. On rocks, Tarbert (110*) Marq.

P. glomerata (Ach.) Schaer. Encrusting mosses on limestone maritime rocks, Hallaig (104*). In a four-spored ascus the spores measured about $110 \times 40\mu$; when there were two spores only they were larger, up to $150 \times 55\mu$.

Acarospora verruciformis Magn. Near Auchmithie (90*). New to Scotland.

- A. atrata* Hue. Near Arbroath (90*).
- Biatorella simplex* (Dav.) B. and R. Invermoriston (96*). Ullapool (105*).
- Ramalina fraxinea* v. *ampliata* (L.) Ach. Black Isle (106*); var. *caliciformis* Nyl. Rothiemurchus (96*).
- R. fastigiata* f. *odontata* Hue and f. *minutula* (Ach.) Cromb. Thurso (109*).
- R. pollinaria* f. *humilis* Ach. Near Clacknaharry (96*).
- R. polymorpha* v. *emplecta* Ach. Corrie Ardrain (88*) E. C. W.
- R. cuspidata* (Ach.) Nyl. Near Rosemarkie (106*).
- R. curnowii* Cromb. Near Inverkirkaig (108*) U.D.; var. *armorica* (Nyl.) Harm. Flyday, Lewis (110*) Marq.
- Lecania albariella* (Nyl.) Muell. On calcareous garden-wall at Arbroath (90*). New to Scotland.
- L. hutchinsia* (Nyl.) A. L. Sm. Arbroath (90*). The thallus is whitish and the paraphyses are scarcely subdiscrete, but as Smith includes both *Lecidea accessitans* Nyl. and *L. albocarnea* Nyl. with whitish thalli and paraphyses not subdiscrete, in *L. hutchinsia* there seems to be no reason for excluding Miss Duncan's specimen with such characters since other characters are more agreeable for it than for *L. erysibe*. The substratum was Old Red Sandstone which was not calciferous.
- L. prosechoides* (Nyl.) Oliv. Dingwall (106*). According to Magnusson this is *Lecanora helicopis* (Wahl.) Ach., its spores being really simple. There is sometimes an apparent septum shown, but usually all trace of it disappears on treatment with caustic potash.
- Biatorina atropurpurea* (Schl.) Mass. Near Inverary (96*).
- B. cristata* A. L. Sm. On a specimen of *Lecanora sulphurea* from Redhead (90*). It is a fungal parasite and is now called *Scutula cristata* Sacc.
- B. stereocaulorum* A. L. Sm. On *Stereocaulon denudatum*, Ach-nashen (106*). This is another fungal parasite (*Scutula stereocaulorum* Krb.).
- Catillaria chalybeia* (Borr.) Mass. Near Bonar Bridge (108*) U.D. Port of Ness (110*) Marq.
- Icmadophila ericetorum* (L.) Zahl. Near Kilmuir, Black Isle (106*).
- Toninia caradocensis* (Leight.) Lahm. Arbroath (90*). This was erroneously given in Lichen Notes III (*Trans.*, 1942, 188) as *Psora friesii*. As the plant was without apothecia I was not quite satisfied about it so asked Miss Duncan to try and find some fruiting material. She was successful in doing so, and the

- spores were found to be 3-septate and not simple as they should be in *Psora friesii*. It is new to Scotland.
- Bilimbia naegelii* (Hepp) Anzi. Dochgarroch (96*).
- B. effusa* Auersw. Evanton (106*).
- Bacidia inundata* (Fr.) Krb. Glen Nevis (97*) W. Young.
- B. arceutina* (Ach.) B. and R. Evanton (106*).
- Placodium granulosum* (Müll.) Hepp. Auchmithie (90*).
- Caloplaca* citrina* var. *flavocitrina* (Nyl.). Portree (104*) Linds.
- C. caesiorufa* (Ach.) Zahl. Near Bonar Bridge (108*).
- C. turneriana* (Ach.). Ethie Haven, near Arbroath (90*).
- C. ferruginea* var. *festiva* (Ach.). Near Bonar Bridge (108*). Laig Bay, Eigg (104*) Marq.
- Pseudophyscia speciosa* (Wulf.) Müll. Carr Bridge (96*).
- Physcia pulverulenta* var. *venusta* (Ach.) Nyl. Culcabock (96*).
- P. aipolia* (Ach.) Nyl. Dochgarroch (96*) and Black Isle (106*).
- P. grisea* (Lam.) Zahl. var. *alphiphora* (Ach.) Lynge. Near Beaully (96*).
- Rinodina exigua* (Ach.) Gray. Dochgarroch (96*).
- R. demissa* (Krb.) Arn. Near Bonar Bridge (108*).
- Buellia spuria* (Schaer.) Krb. Near Perth (89*) Linds.
- B. verruculosa* (Borr.) Mudd. Newburgh (85*) and Dalwhinnie (96*) Linds.
- B. aethalea* (Ach.) Th. Fr. Dalwhinnie (96*) Linds. There is a plant very similar to this except that it does not give a coloration with K. It has been met with in several localities in our islands and occurred in some material from Braemar (92). Nylander gave this form the name of *B. aethalioides*.
- B. stellulata* (Tayl.) Mudd. Dalwhinnie (96*) Linds.
- B. schaeferi* DN. On larch, Cawdor Woods, near Nairn (96*).
- B. myriocarpa* form *stigmatea* Krb. Redhead (90*) leg. Croall!
- B. colludens* (Nyl.) Arn. A plant collected by Marquand at Suanaral, Lewis (110*), may go under this species as a form or variety with a more ochraceous thallus and larger apothecia than usual.
- Rhizocarpon geographicum* var. *atrovirens* (L.) Krb. Inverfarigaig (96*).
- R. confervoides* form *dispersum* (Leight.) A. L. Sm. Glen Nevis (97*) W. Young. This may go under *R. reductum* Th. Fr. of continental authors.

* I should prefer following Massalongo, Koerber and Mudd in using *Calopisma* as the generic name for the species given under *Caloplaca* though a strict interpretation of International Rules is against such use.

- R. reductum* Th. Fr. Specimens collected by Lauder Lindsay from the top of Norman Law (85*) and Craig Rossie (88) may also go under this species.
- R. petraeum* var. *excentricum* (Ach.) A. L. Sim. Hill of Findhaven (90*) Linds.
- R. obscuratum* (Ach.) Mass. Suanaral, Lewis (110*) Marq.; form *ferratum* (Nyl.) A. L. Sm. Glen Fee (90*) W. Young. A plant collected by Miss Duncan on schistose rocks near Invermoriston (96) was placed by her under this species, but it is not the usual form. It agrees quite well with the description of var. *elegans* Eitner, a variety which had not been recorded from our islands. The flattish areolae of the thallus are usually scattered and seated on a dark hypothallus. The black apothecial discs are smaller (0.5–0.6 mm.) than they are in the type and have their proper margins similarly coloured. The spores are colourless at first but become dark later, are $29\text{--}35 \times 9\text{--}14 \mu$ and are about 14-celled. The appearance of the plant is more like a *Lecidea*.
- R. rubescens* Th. Fr. On rocks, Cuillin, Skye (104*) Marq. For the nomenclature of this lichen see Lichen Notes III (*Trans.*, 1942, 200).
- Gyrophora erosa* (Web.) Ach. Glen Dole, Clova (90*). The medulla gives no coloration with calcium hypochlorite.
- G. polyrrhiza* (L.) Krb. On rocks near the King's House (96*) Marq.
- G. polyphylla* (L.) Hook. Glen Doll (90) W. Young. This is in part var. *glabra* (Ach.) Th. Fr. = form *monophylla* Leight.
- Umbilicaria pustulata* (L.) Hoff. Stenton Crag, Dunkeld (89*) E. C. W.
- Thelotrema lepadinum* Ach. On bark of young oak, near Evanton (106*).
- Cladonia cyathomorpha* Wats. Near Loch Brandy (90*) W. Young.
- C. pyxidata* var. *chlorophaea* Flk. Ardlui (99*).
- C. strepsilis* (Ach.) Wain. On moist peaty soil near Meall Ivarvunie, Loch Ness (96*).
- C. pityrea* (Flk.) Fr. Black Isle (106*).
- C. cervicornis* f. *phyllocephala* Flot. On rocks, west side of Baelach Raonasgail, Lewis (110*) Marq.
- C. ochrochlora* Flk. form *phyllostrota* Flk. Woodhall (77*) R. Burn.
- C. cariosa* (Ach.) Spreng. On damp peat near L. Kinnord, Dinnet (92*).
- C. squamosa* var. *muricella* Del. Glen Esk (90*) W. Young.

- Pycnothelia papillaria* (Ehrh.) Duf. Invermoriston (96*); mostly form *molariformis* (Hoff.) from Fuarvonja (96*).
- Baeomyces placophyllus* Ach. On soil, Invermoriston (96*).
- Pilophorus cereolus* (Ach.) Th. Fr. Above Invermoriston (96*).
- Stereocaulon denudatum* Flk. Mauchline (75*) leg. Abbot! Ach-nashen (106*); form *capitatum* Flot. Invermoriston (96*).
- S. condensatum* Hoff. Achnashen (106*).
- S. nanum* Ach. On soil, near Kilmuir (96*).
- Pachyphiale corticola* Lönnr. Killin (88). The only previous record from the British Isles was by Crombie from Craig Calliach on a trunk of pine. Miss Duncan's specimen was obtained from a sycamore at a much lower altitude (Finlarig).
- Racodium rupestre* Pers. On rocks, Trislaig, near Fort William (97*) W. W.
- Crocynia libricola* B. de Lesdain. On old stump, Maspie Den, Falkland (85*) W. Young. The thallus was not so green as usual, but as the specimen was collected in 1931 the paler colour may be attributed to drying.
- C. flava* (Ach.) Hue. On trees, Inverness (96*) and Avoch (106*).
- Lobaria laetevirens* (Light.) Zahl. On trees, Laig, Eigg (104*) Marq. Associated with *Parmeliella plumbea* and the isidioid form named *P. atlantica* Deg. One of Crombie's specimens of *P. plumbea* from Appin (98) also contains the two forms.
- Parmeliella corallinodes* form *nigricans* (Light.) A. L. Sm. Near Inverary (96*); var. *incrassata* (Nyl.) A. L. Sm. Strathglass (96*).
- Nephromium lusitanicum* (Schaer.) Nyl. Dunure, with form *panniforme* Cromb. (75*) E. C. W. A panniform condition of the var. *hibernicum* Nyl. occurs at Fort William (97) W. W.
- Placynthium nigrum* var. *psotinum* (Ach.) Trevis. Ullapool (105*).
- Leptogium burgesii* (Light.) Mont. On trees near Falls of Foyers (96*).
- L. hildenbrandii* (Garov.) Nyl. Finlarig, Killin (88). If the segregation of this from its allies is warranted, the somewhat granulose upper surface of the thallus and the long rhizinae in the central portion of the lower surface bring Miss Duncan's specimen to it. The upper surface is often furfuraceous, and Harmand gives this form as var. *furfuracea* (88*).
- Synechoblastus nigrescens* (Huds.) Anzi. Dailly (75*) F. A. Sowter.
- S. aggregatus* (Ach.) Th. Fr. Kiltarlity, near Beaully (96*). This specimen has a general resemblance to *S. fascicularis*, but the spores are much too long for the latter species.

- Collema tenax* (Sw.) Sm. Dunkeld (89*) Linds. Another specimen in Herb. Edinb. collected by Carroll from a calcareous substratum exposed to the spray of water had a much more compact medulla than usual and appeared to be *C. cheileum*, but the compact appearance is not due to the abundance of hyphae but to the prolific formation of algae which occur in both long and short chains. No vertical hyphae, which usually occur in *C. cheileum*, were seen.
- C. pulposum* (Bernh.) Ach. The well-developed plant known as form *formosum* (Ach.) Nyl. Kinnoul Hill (89*) Linds.
- C. ceranoides* (Borr.) Nyl. Kinnoul Hill (89*) Linds.
- C. cheileum* Ach. Elie (85*) Linds.
- C. multifidum* (Scop.) Schaer. Glen Beag (87*) D. A. Jones.
- Polychidium muscicolum* (Sw.) Gray. Glenmoriston (96*).
- Arthonia didyma* Krb. Inverfarigaig (96*).
- A. gregaria* (Weig.) Krb. Inverquharity (90*); var. *astroidea* (Leight.) Mudd. Drumnadrochit (96*); var. *anerythrea* (Nyl.) A. L. Sm. Evanton (106*).
- A. radiata* var. *swartziana* (Ach.) Sydow. Black Isle (106*).
- A. asperella* Leight. Cortachy (90*).
- A. punctiformis* var. *melantera* (Ach.) Leight. Inverfarigaig (96*).
- Opegrapha confluens* Stiz. Parkhill, near Arbroath (90*).
- Graphis scripta* (L.) Ach. Drumnadrochit (96*).
- G. elegans* (Ach.) Borr. Near Evanton (106*).
- G. ramificans* Nyl. Near Evanton (106*). New to Scotland. By some authors this is placed under *Phaeographis* because there is a tendency for the spores to become brown, the paraphyses to be darker at the tips and the hypothecium to be faint brownish.
- Chaenotheca acicularis* (Sm.) Zwack. Avoch (96*).
- C. chrysocephala* var. *filaris* (Ach.) DT. and S. Tomich (96*).
- Calicium hyperellum* f. *balium* (Ach.) Nyl. Near Beaully (96*).
- Stenocybe byssacea* (Fr.) Nyl. On alder, Kirriemuir (90*).
- Coniocybe furfuracea* (L.) Ach. Near Avoch, Black Isle (106*).
- Cypheium stigonellum* Zahl. Ben-y-Vrackie (89). The specimen apparently has been correctly referred to the plant bearing this name in A. L. Smith's Monograph. *C. stigonellum* is said to be parasitic on the thallus of a *Pertusaria*, whereas in Miss Duncan's specimen the thallus appears to be that of *Biatora coarctata*, in which some incipient attempts have been made to form apothecia, as there are some indications of the formation of an epithalline margin and of a blue coloration to the

hymenium. Such attempts apparently have been aborted by the attacks of parasitic fungi. The most abundant, though often ill-developed, is one of the Hyphomycetes, *Coniothecium sphaerale* Keissl. In some fructifications, asci with dark brown, one-septate spores ($8-12 \times 6-7\mu$) occur and these seem to belong to one of the Pyrenomycetes, *Discothecium gemmiferum* Vouaux. In true *Cyphelia* a mazedium (a loose mass of spores at the surface of the apothecium) is present. On rubbing the apothecia with white paper a dark mark is made, but this does not occur in the specimen.

Sphaerocarpus melanocarpus (Sw.) Schaer. Ullapool (105*).

Dermatocarpon minutum (L.) Th. Fr. Girvan (75*) F. A. Sowter; var. *complicatum* (Sw.) Th. Fr., Iona (103*) L. B. Trotter; f. *decipiens* A. L. Sm., Ben Doran (98*) W. Young. The last-named is given by some authors as a variety of *D. polyphyllum* (Wulf.) DT. and S.

Verrucaria papillosa Ach. and *V. aethiobola* Wahl. have been seen in material from near Lewiston (96*) W. W. *V. maura* Wahl. has been noted by Dr. Lamb from 110.

V. nigrescens Pers., *V. muralis* Ach. and *V. calciseda* DC. emend. Stein. were on stones collected by Marquand from Laig Bay, Eigg, and all are new records for v.c. 104.

Thelidium impressum (Naeg.) Mull. On rock, foot of Morrone (92*). New to Scotland.

Polyblastia schraderi (Sm.) A. L. Sm. Foot of Morrone (92*).

P. cupularis Mass. Specimens referable here have been received from rocks, Ben Lawers (88) and Ben Lomond (89). The species is probably a form of *P. intercedens* and does not merit a specific status. The Ben Lawers plant may come under *P. inumbrata* (Nyl.) A. L. Sm. (if that species is allowable) with spores smaller and with little signs of involucrellum.

Arthopyrenia fallax (Nyl.) Arn. and *A. epidermidis* (Fr.) Mudd. Ullapool (105*).

A. pyrenastrella (Nyl.) Oliv. Inverfarigaig (96*).

A. submicans (Nyl.) A. L. Sm. Trislaig, near Fort William (97*) W. W.

A. rhyponia (Ach.) Mass. Craigendarroch, Ballater (92*). Trislaig (97*) W. W.

A. microspila Krb. Black Isle (106*). Reference was made to this supposed *Arthopyrenia* in my last lot of notes (*Trans.*, 1942, 208) as being a fungus. It is now generally admitted to be a fungus parasitic on the thallus of a lichen and has received

the name of *Pharcidia microspila* (Krb.) Wint. Apparently the lichen host was practically absent in Hardy's plant from Penmanshiel.

Leptorhaphis carrollii A. L. Sm. On young oak near Evanton (106*).

Porina leptalea (D. and M.) A. L. Sm. Near Inverfarigaig (96*).

P. carpinea (Pers.) Zahl. N.E. coast of Rum (104*) Marq.

P. chlorotica (Ach.) Wain. Near Bonar Bridge (108*).

Melanotheca gelatinosa (Chev.) Nyl. Cortachy (90*). The spores as figured in A. L. Sm. Brit. Lich. are relatively too narrow and do not show the median constriction which is often present.

Mycoporum quercus (Mass.) Mull. Ullapool (105*).

VITAMIN B1 CONTENT OF ARCTIC PLANTS AND ANIMAL TISSUE.

By KAARE RODAHL (Institute of Physiology, University of Oslo).

(Read 17th May 1945.)

In a previous paper (1) attention was called to the fact that during the dark period of the year (November–February) the European trappers in North-East Greenland generally showed symptoms of debility and inertia, and complained of lack of initiative. It was suggested that this might be due to a mild form of avitaminosis C, following a decreased food intake during this period. The concentration of ascorbic acid in the blood of some European hunters from a winter expedition to Greenland was determined by Høygaard and Rasmussen (2) by the technique of Emmerie and Van Eckelen. In 9 cases out of 12 the concentration was less than 0.5 mg. ascorbic acid per 100 ml. blood, which must be considered as subclinical scurvy. Apart from one case of beri-beri (in the Captain) there were no clinical signs of deficiency at the time of examination (August). It was reported that potatoes were finished in March and lemons by Christmas time. There was reason to believe that the marked lack of appetite and chronic fatigue observed might be explained as a result of vitamin B1 deficiency. It was also shown that the European trappers in Greenland are on a B1-deficient diet throughout the whole year. In view of this, and in an attempt to increase the knowledge on vitamin sources in the Arctic, samples of arctic plants and animal organs were collected during a scientific expedition to North-East Greenland, 1939–40, organized by the author, under the auspices of the University of Oslo. The vitamin B1 in the samples was assayed at the Dunn Nutritional Laboratory, Cambridge, England, immediately after the return of the expedition in the autumn of 1940.

TECHNIQUE.

1. *The conservation of vitamin B1* was done by the following two methods:—

(1) 100–1000 gm. (in the case of plants, about 10 gm. were finely chopped) material were minced, 2–5 ml. 1 per cent. hydrochloric acid added, the mixture soaked with toluene, and the whole transferred to tins containing approximately 10 ml. toluene per 100 gm.

material. Finally the lids were firmly secured by binding with adhesive tape, and stored in a cool, dry place.

(2) 10–25 gm. (in the case of plants, 5–10 gm.) of material were finely chopped or minced and 80–100 ml. 1 per cent. hydrochloric acid added. The mixture was heated to the boiling-point, cooled and filtered, the residue being rinsed with 2–5 ml. 1 per cent. hydrochloric acid. 2 gm. “Franconit” was then added to the filtrate, and the solution was shaken vigorously for one hour, after which it was filtered and washed with 5 ml. distilled water. The complete residue was dried in air, carefully weighed, and transferred quantitatively to special small flasks with cork and paraffin seal. Treated in this way the samples should be able to keep indefinitely when stored in a cool, dark place.

2. Estimation of vitamin B1.

(1) *In Minced Material*.—10 gm. material in toluene was used, and the aneurin determined by the thiochrome method (L. J. Harris and Y. L. Wang, *Bioch. J.*, xxxv, 1050 (1941)). In the case of dry weight determinations, 25 gm. were used.

(2) *In Adsorbate*.—From each specimen the vitamin B1 in each of three 50-mg. samples of adsorbate was determined by the technique mentioned above (3). The vitamin B1 was eluted in alkaline solution, oxidized to thiochrome by means of ferricyanide, and the thiochrome concentration was measured by the blue fluorescence (4).

RESULTS.

The results are shown in the following tables:—

TABLE I.
VITAMIN B1 CONTENT IN ORGANS FROM SOME ARCTIC
ANIMALS AND BIRDS.

Animal.	Organ.	Gamma Vit. B1 per gm. Dried Substance.	Gamma Vit. B1 per gm. Fresh Organ.
Musk Ox (<i>Ovibos moschatus</i>).	Muscles, fresh.	1·70	0·50
	Heart muscles.	9·37	2·81
	Tongue.	1·92	0·98
	Liver.	11·27	3·04
	Brain.	3·13	0·63
	Milk from udder.	0·29	..
	Udder, gland tissue.	13·00	..
	Kidney.	5·51	1·38
	Spleen.	29·57	..

TABLE I—continued.

Animal.	Organ.	Gamma Vit. B1 per gm. Dried Substance.	Gamma Vit. B1 per gm. Fresh Organ.
Musk Ox (<i>Ovibos moschatus</i>).	Testis.	4.24	..
	Epididymis.	0.00	0.00
	Testis and epididymis.	1.55	..
	Stomach.	0.00	0.00
	Content of stomach.	0.00	0.00
	Small intestine.	0.49	0.14
	Content of small intestine.	0.00	0.00
	Lung.	0.34	0.10
	Subcutaneous fat.	0.41	0.38
Fjord Seal (<i>Phoca foetida</i>).	Suet.	0.20	0.00
	Muscles, fresh.	1.14	0.34
	Tongue.	0.16	0.08
	Liver.	4.05	1.09
	Kidney.	6.16	1.54
	Spleen.	..	0.60
	Pancreas.	0.70	..
	Gall-bladder.	0.00	0.00
	Bile.	0.00	0.00
Bearded Seal (<i>Phoca barbata</i>).	Muscles, fresh.	1.14	0.34
	Heart muscle.	9.78	2.91
	Liver.	0.70	0.19
	Kidney.	28.34	7.09
	Subcutaneous fat.	0.21	0.00
Shark (<i>Somniosus microcephalus</i>).	Liver.	1.55	0.82
Nerwhal (<i>Monodon monoceros</i>).	"Mattaq" (epidermis).	17.20	..
Salmon (<i>Salmo alpinus</i>).	Meat.	1.05	0.37
	Liver.	7.14	..
	Roes.	15.24	..
Snow hare (<i>Lepus variabilis glacialis</i>).	Content of stomach.	2.19	..
Rock Ptarmigan (<i>Lagopus rupestris</i>).	Breast muscles.	8.45	3.38
Glaucous-gull (<i>Larus hyporboreus</i>).	Breast muscles.	..	3.37
Parasitic Jaeger (<i>Stercorarius parasiticus</i>).	Intestines and content.	..	1.18
Eider-duck (<i>Somateria mollissima</i>).	Intestines.	0.00	0.00

The above specimens were gathered between 3rd September 1939 and 29th June 1940 in North-East Greenland, and assayed during the period 20th November 1940 to 9th January 1941.

TABLE II.

VITAMIN B1 CONTENT IN ORGANS OF ARCTIC ANIMALS AND BIRDS, AS DETERMINED BY THE THIOCHROME METHOD IN "FRANCONIT" SAMPLES.

Species.	Organ.	Gamma Vit. B1 per gm.
Musk Ox (<i>Ovibos moschatus</i>).	Meat, fresh.	0.56
	„ stored 2½ months.	0.30
	„ salted.	0.55
	„ fried.	0.15
	„ boiled.	0.04
	Liver, fresh.	1.05
	„ fried.	0.34
	Kidney.	0.93
	Kidney, medullary substance.	0.48
	„ cortical.	0.58
	Brain (calf).	0.07
	Nerves (Plexus brachialis).	0.16
	Eye.	0.37
	Pancreas.	0.65
	Spleen.	0.29
	Thyroid glands.	1.20
	Suprarenal glands.	1.61
	Bile from gall-bladder.	0.22
	Small intestines.	0.36
	Content of small intestines.	0.33
	Suet.	0.13
	Content of stomach.	0.23
	Subcutaneous fat.	0.11
Shark (<i>Somniosus microcephalus</i>).	Liver.	0.10
	Meat.	0.04
Parasitic Jaeger (<i>Stercorarius parasiticus</i>).	Liver.	0.12
Loon (<i>Gavia imber</i>).	Liver.	0.95
Eider-duck (<i>Somateria mollissima</i>).	Liver.	0.48
	(Egg).	0.23

TABLE III.

VITAMIN B1 CONTENT IN SOME COMMON GREENLAND PLANTS, AS DETERMINED BY THE THIOCHROME METHOD IN "FRANCONIT" SAMPLES.

Plant.	Part of Plant Analysed.	Gamma Vitamin B1 per gm.
<i>Honckenya peploides</i> (L.) Ehrh.	Whole plant	0.13
	New buds	0.21
<i>Salix</i> sp.	Buds	0.85
	Stems	0.43
	Flowers	0.31
	Leaves	0.31
<i>Betula nana</i> L.	Buds	3.50
	Stems	2.30
	Leaves	0.32
<i>Saxifraga oppositifolia</i> L.	Whole plant	0.69
<i>Dryas octopetala</i> L.	Whole plant	0.04
<i>Papaver radicum</i> Rottb.	Whole plant	0.19
<i>Cassiope tetragona</i> (L.) D. Don	Whole plant	traces
Heather	Whole plant	0.17
<i>Arnica alpina</i> (L.) Olin	Whole plant	0.02
<i>Potentilla nivea</i> L.	Whole plant	0.33
<i>Oxyria digyna</i> Hill	Whole plant	0.45
<i>Epilobium angustifolium</i> L.	Whole plant	0.20
	Flowers	0.21
<i>Lychnis triflora</i> R.Br.	Whole plant	0.57
<i>Pedicularis hirsuta</i> L.	Whole plant	0.15
<i>Armeria</i> sp.	Whole plant	0.36
<i>Cerastium alpinum</i> L.	Whole plant	0.19
<i>Alopecurus alpinus</i> Sm.	Whole plant	0.02
<i>Saxifraga cernua</i> L.	Whole plant	0.25
<i>Saxifraga nivalis</i> L.	Whole plant	0.26
<i>Agaricus</i> sp.	Whole plant	0.40

It must be observed that of the samples investigated only *Betula nana* appeared to have any significant Vitamin B1 content.

It will be observed that none of the sources mentioned except roe of salmon and "mattaq" can supply the necessary amount of vitamin B1 when eaten in normal quantities. Not more than 300 gm. of meat is consumed per man per day, even during hard work, or travelling of long duration. The average sized musk ox (including internal organs) provides approximately 20,000 I.U. vitamin B1. The internal organs alone provide approximately 4000 I.U., which should be equal to 10 days requirement.

Of the European foodstuffs brought up to the trappers in North-East Greenland, bread, eggs, sardines, potatoes, ham, peas, and beans are of most value from the standpoint of vitamin B1 supply.

However, when one takes into consideration the relatively high consumption of fat and protein by the people, the actual requirement of vitamin B1 may be considerably lower than the amount recommended by the League of Nations (300 I.U. per day).

In the month of March the base was visited by a trapper (Ö. T., age 25 years) who had spent the two previous winters alone trapping at Peters Bay (lat. 76° N.). During the whole winter he had suffered from anorexia. His diet was very little varied, and consisted mainly of salted or fried meat, potatoes, white bread and coffee. Very little of internal organs of newly slaughtered animals was consumed, and no dark bread or eggs.

During the last month he had oedema and itching of the legs, calf muscle cramps, and occasionally signs of heart trouble. During a fortnight he was given dried yeast, one teaspoonful daily. At the end of this period urine samples were collected from the patient, and also from three normal persons. (Unfortunately, because of technical difficulties, urine samples from Ö. T. could not be conserved before the patient was given dried yeast.) 24-hour sample was collected, hydrochloric acid added, and shaken with 2 gm. "Franconit" for one hour. The "Franconit" adsorbate was dried, and the thiamine determined by the thiochrome method (3, 5, 6, 7).

The following results were obtained:—

Ö. T.	age 25 years.	0.12 gamma/ml.	or appr. 44 I.U.	24 hours urine.
H. S.	" 22 "	0.05	" "	15 " "
S. N.	" 36 "	0.07	" "	20 " "
H. R.	" 51 "	0.01	" "	4 " "

The very high excretion of vitamin B1 in Ö. T. can easily be explained by the ingestion of dried yeast. The excretion in H. S. and S. N., who both were living on an average diet, may, according to Harris *et al.* (6), be considered normal. H. R. did not show any

symptoms of deficiency, but was less active and had lower food consumption than the rest of the individuals examined.

In view of the importance of these questions, clinical tests should be carried out on these people on an improved diet.

ACKNOWLEDGMENTS.

My thanks are due to the director of the Dunn Nutritional Laboratory, Cambridge, Dr. L. J. Harris, and to Sir Charles Martin, for the valuable help and criticism, and for providing laboratory facilities to continue the research after my return to England. My thanks are also due to Dr. Wang and Dr. Kodicheck for valuable technical advice. A number of the vitamin B1 analyses in Franconit samples are done by Dr. Kodicheck. Further, my thanks are due to the director of the Institute of Physiology, University of Oslo, Dr. E. Langfeldt, and the following scientific funds: Det Medisinske Fakultets Videnskapelige Fonds, Nansenfondet, Varekrigs Forskningsfond, and Freiafondet,—with whose assistance the expedition came into existence.

Unfortunately, due to war conditions, it has not been possible to submit this paper to the staff chief of the laboratory in Oslo before publication.

DISCUSSION.

As the aneurin could not be assayed in the field laboratory, it was impossible to determine if any deterioration had taken place in the collected samples. However, the same procedure of preservation has been used on previous occasions at Hermetikk-industriens Laboratorium, Stavanger, Norway, and no deterioration was found to have taken place at the end of the three months' storage (personal communication, G. Lunde). The vitamin B1 content of organs of Arctic animals preserved in toluene compare favourably with the vitamin B1 content in similar European and American foodstuffs.

In some cases there was a reasonable agreement in the results obtained in the same organs treated with toluene, and adsorbed on "Franconit" (fresh muscles, kidney suet). In the majority of cases, however, the figures obtained by the "Franconit" technique are lower than in the same organs preserved in toluene. This might be explained by an incomplete elution in the alkaline solution.

Of the organs examined, the liver, kidney, and heart appeared to be the best sources of vitamin B1. The breast muscles of the Arctic birds also had an appreciable amount of vitamin B1. The roe of

salmon and "mattaq" was found to have an extremely high concentration of vitamin B1. The "mattaq" (skin of the narwhal) has also a high vitamin C concentration, and has been known for a long time as a very good antiscorbutic.

The following table shows the amount of animal organs (raw) necessary to secure the daily requirement of vitamin B1 per individual (300 I.U.):—

Source of Vitamin B1.	Gm. to be Consumed.	Total Weight of Organ, gm.
Heart muscle (musk ox) . . .	400	1000
Liver " . . .	400	2500
Kidney " . . .	800	230
Trunk muscle . . .	4000	..
Breast muscle (ptarmigan) . .	400	..
"Mattaq" (narwhal) . . .	120	..
Roe (salmon) . . .	120	..

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THE MOSS FLORA OF THE ISLAND OF RHUM, V.C. 104. By W. A. CLARK, B.Sc., Ph.D., and R. B. COOKE, M.Sc., Dept. of Botany, King's College, Newcastle upon Tyne. (With Plate III.)

(Read 14th June 1945.)

In 1939 Dr. K. B. Blackburn and Miss E. M. Lobley published a list of the Bryophytes of the Small Isles Parish of Inverness-shire and of the Isle of Soay (Proc. Univ. Durham Phil. Soc., vol. x, pt. 2, 1939). The mosses (excluding Sphagnales) in this list number 139 species and varieties, of which 83 are recorded from Rhum. Through the kindness of Lady Bullough, the authors have been fortunate enough to be able to make several spring and summer visits to the Island of Rhum during the period 1941-44, and on these occasions our efforts were largely concentrated on the mosses. As a result the number of species and varieties from this island has been increased to 277.* At the same time much information has been gained concerning the general distribution of the mosses on Rhum, and it is for these reasons that the present paper has been prepared.

Of the species and varieties obtained, *Andreaea Hartmani* Thed., collected and already recorded by Prof. J. W. Heslop Harrison (Journ. Bot., vol. lxxx, No. 950, 1942), and *Weisia curvirostris* var. *cataractarum* Schp. are new to the British Isles, while a further 77 are new to v.c. 104. That such a small island as Rhum should possess such a rich moss flora is not surprising when one considers its mountainous nature, its varied geological structure, and its moist equable climate, all of which acting together produce a large variety of habitats. The "alpine" nature of the island can be gauged by the finding of such species as *Ditrichum zonatum*, *Ditrichum vaginans*, *Cynodontium virens*, *Dicranum fulvellum*, *Leptodontium recurvifolium*, *Webera commutata*, *Plagiothecium Muellerianum*, and *Hypnum molluscum* var. *robustum*.

While it is hoped in a later paper to discuss more fully some of the problems concerning the distribution of the Rhum mosses, the opportunity is taken here to mention some points of special interest concerning the flora as a whole. Firstly, attention is directed to

* This number includes two species and one variety not yet collected by the present authors, but listed by Blackburn and Lobley.

two areas, characterised by the richness of the flora they support. The basic mugearite cliffs of Fionchra and Bloodstone Hill constitute the first of these, and they provide the centre for a group of species of which the most interesting are *Barbula tophacea* and its var. *acutifolia*, *Encalypta ciliata*, *Bryum roseum*, *Mnium stellare*, *Rhabdoweisia fugax*, *Grimmia patens*, *Barbula rubella* var. *ruberrima*, *Barbula cylindrica*, *Weisia crispata*, *Anoetangium compactum* var. *pellucidum*, *Zygodon lapponicus*, *Plagiobryum Zierii*, *Pterogonium gracile*, and *Antitrichia curtipendula*. The first five of these are apparently confined to these cliffs; the others occur rarely elsewhere and then again usually on peridotite or other basic igneous rock. Mugearite, on weathering, breaks down to form innumerable ledges and a fairly highly basic soil in which both the pH (7.24) and the exchangeable calcium are high, conditions which no doubt account for the mosses and the rare flowering plants found there.

The second area includes Salisbury Dam and its neighbourhood, and from this locality the following interesting species have been recorded: *Archidium alternifolium*, *Cynodontium Jenneri*, *Dicranella secunda*, *Dicranella rufescens*, *Dicranella varia*, *Barbula rubella* var. *ruberrima*, *Weisia microstoma*, *Weisia crispata*, *Weisia tenuis*, *Weisia calcarea* var. *viridula*, *Webera annotina* and its var. *erecta*, *Webera prolifera*, *Bryum concinatum*, and *Bryum turbinatum*. This old dam, now empty, is situated just north of the point where the stream running north from the Long Loch joins that from Monadh Mhiltich. Before entering the dam area these streams run through fairly deep ravines with steep, sheltered, rocky banks. The geology of this region is complex, for in this comparatively small area the following types of rock occur: granite, Torridonian sandstone, and peridotite, together with considerable quantities of glacial drift. Many factors contribute to making this area ideally suitable for moss species. It is in the first place extremely sheltered, while in the second place a large variety of rocks is provided by its diverse geological nature. Of equal importance, however, is the fact that the predominating rock and glacial drift are soft and crumbly and weather readily; in this way many bare surfaces are produced which prove too unstable for the establishment of flowering plants but which are readily colonised by mosses.

In addition to the ultrabasic and basic igneous rocks which are well represented on Rhum, Torridonian sandstone and limestone also occur. The greater part of the northern half of the island consists of the former, but the latter is small in amount and confined to the north-west of the island in the Monadh Dubh region. These

outcrops of limestone provide the habitats for several lime-loving species including *Grimmia orbicularis*, *Weisia curvirostris* var. *cataractarum*, *Weisia verticillata*, *Encalypta streptocarpa*, and *Orthothecium rufescens*.

From the point of view of rarity elsewhere in Britain, the following species and varieties are worthy of special mention: *Campylopus Shawii*, *Weisia curvirostris* var. *insignis*, *Trichostomum hibernicum*, *Ditrichum vaginans*, *Cynodontium virens*, *Campylopus atrovirens* var. *falcatus*, *Bryum concinnatum*, *Myurium hebridarum*, *Plagiothecium Muellerianum*, and *Hypnum molluscum* var. *robustum*. All, with the exception of *T. hibernicum* which is common, were recorded from one station only, while the first three are, in addition, endemic to Britain.

The rarity of *Myurium hebridarum* on Rhum is in striking contrast to its abundance on Barra, S. Uist, and Benbecula in the Outer Hebrides, v.c. 110; further, its station on Rhum is unusual in that it is situated at a height of about 1600 feet on the east side of Orval. Dixon in the "Student's Handbook of British Mosses" describes the habitat of this moss as "near the coast on earth among rocks". Watson reports that it occurs in similar situations along the east and west coasts of Barra and that it is absent from the high ground in the central hills, though it ascends for several hundred feet on all the western hill slopes examined ("The Mosses of Barra, Outer Hebrides", Trans. and Proc. Bot. Soc. Edin., vol. xxxii, pt. iv, 1939). Its occurrence on Rhum at this altitude is made all the more interesting because it was also found at about the same elevation at the head of Glen Liadale on the east side of Ben Mhor, S. Uist, v.c. 110. This station was discovered by the authors last summer and here *Myurium* was growing in association with such plants as *Sedum roseum*, *Oxyria digyna*, *Armeria maritima*, *Festuca ovina* var. *vivipara*, *Saxifraga stellaris*, *Solidago Virgaurea*, *Veronica officinalis*, *Thalictrum alpinum*, *Hymenophyllum unilaterale*, and *Cystopteris fragilis* (see Plate III). As there is a strong possibility that the upper part of Ben Mhor was free from ice during the period of maximum glaciation (Jehu and Craig, Trans. Roy. Soc. Edin., vol. liii, pt. iii, no. xxx), the occurrence of *Myurium* with Arctic-Alpine plants acquires a new significance. The discontinuous distribution of *Myurium*—found outside Britain only in the Azores and Canary Islands—indicates that the species is of considerable age, and points to a preglacial origin for this moss in Britain. On the evidence presented, survival of this species on Ben Mhor and Orval during the Ice Age must be considered as a distinct possibility. On the retreat of the ice it



Myrium hebridarum growing at an altitude of 1500 feet on the cliffs at the head of Glen Liadale, S. Uist. (See p. 254.)

would descend to occupy its better known habitats at lower elevations around the coast.

The lack of cultivated land on Rhum is reflected in the almost complete absence of mosses of cultivation from our list. The sand dune representatives are also poor in number as compared with other Hebridean lists, but this, too, is due to the small extent of sandy ground on the island.

Lastly, a feature of special note is the fruiting on Rhum of some species in which this condition is seldom encountered. Fruiting specimens of *Grimmia trichophylla*, *Zygodon Mougeotii*, *Breutelia arcuata*, *Mnium undulatum*, and *Eurhynchium Swartzii* were all observed, and it seems probable that one of the factors responsible is the dampness of the climate.

All the critical species and varieties have been checked and confirmed by Mr. J. B. Duncan, for whose invaluable assistance and encouragement we cannot be sufficiently grateful. Our thanks are also tendered to Prof. J. W. Heslop Harrison, the leader of our party, and to the Research Committee of King's College, Newcastle upon Tyne, for the grant which enabled this work to be carried out.

In the following list the nomenclature of the Census Catalogue of British Mosses (2nd ed.), 1926, has been used. Species and varieties indicated by an asterisk are, according to Mr. J. B. Duncan, new to v.c. 104.

LIST OF MOSSES.

Andreaea petrophila Ehrh. Mountain rocks, common.

*var. *alpestris* Thed. Much rarer than the last; recorded from Ruinsival, Black Hill, Glen Shellesder, and Monadh Dubh.

**A. Hartmani* Thed. Found by Prof. J. W. Heslop Harrison in an isolated locality on the south-east slopes of Hallival.

A. alpina Smith. Equally as common as *petrophila*, in similar situations.

A. Rothii Web. and Mohr. Less frequent than the foregoing, and not yet found on any of the hills on the west side of the island.

*var. *falcata* Lindb. Has only been found on Hallival, and at the unusually low altitude of 50 feet near Kinloch.

Tetraphis pellucida Hedw. In Mr. C. V. B. Marquand's list for Rhum, and given in Dr. Blackburn's list, but not yet found by the authors.

Catharinea undulata Web. and Mohr. In shady situations, local.

- Oligotrichum hercynicum* Lam. Not uncommon on bare stony mountain slopes.
- Polytrichum nanum* Neck. Only recorded from Barkeval, Askival, and Orval.
- P. aloides* Hedw. Occasionally on sandy and peaty banks.
- P. urnigerum* L. Here and there on gravelly slopes.
- P. alpinum* L. Locally plentiful on the hills.
- P. piliferum* Schreb. Equally as plentiful as the last, but in drier situations.
- P. juniperinum* Willd. Observed only on stony ground at Kinloch and Harris, but no doubt overlooked elsewhere.
- P. formosum* Hedw. On a steep bank among heather on Barkeval, and near the school at Kinloch.
- P. commune* L. Generally very common.
- Diphyscium foliosum* Mohr. Frequent enough on dry peaty banks.
- **Archidium alternifolium* Schp. Wet sandy banks, Salisbury Dam.
- Ditrichum homomallum* Hampe. Sandy banks, rare; Salisbury Dam, Orval, and Black Hill.
- **D. zonatum* Limpr. Summit cliffs of Askival, and on the lower western slopes of Trallval facing Glen Harris.
- **D. vaginans* Hampe. This very rare British moss was found on a rock with the previous species on Trallval.
- D. flexicaule* Hampe. Locally abundant on the fixed calcareous dunes at Kilmory and Samhnan Insir; also found elsewhere on stony sandy ground.
- *var. *densum* B. and S. One record only, for the sea cliffs, Monadh Dubh.
- Swartzia montana* Lindb. Crevices of rocks, rather rare.
- Ceratodon purpureus* Brid. Widely distributed in a variety of situations.
- Rhabdoweisia fugax* B. and S. Overhanging dry bank of a stream leading to Askival, and on rocks, Bloodstone Hill.
- **R. denticulata* B. and S. Sandy ground, Orval; cliffs above Black Hill Loch, and on the mugarite cliffs of Fionchra.
- **Cynodontium Jenneri* Stirt. On a peaty bank above Salisbury Dam.
- **C. virens* Schp. Collected once at a low elevation on the south side of Loch Scresort.
- Dichodontium pellucidum* Schp. Wet rocks, etc., frequent.
- var. *compactum* Schp. Askival and Kilmory.
- **D. flavescens* Lindb. At a waterfall north-east of Fionchra, and at Harris.

- Dicranella heteromalla* Schp. Occasionally on sandy banks, and reaching the summit cliffs of Askival.
- **D. secunda* Lindb. Sandy bank of stream running into Salisbury Dam, and on Trallval.
- D. rufescens* Schp. On wet clay along the banks of the stream running north from the Long Loch.
- **D. varia* Schp. Recorded only from Salisbury Dam, on damp crumbly rocks.
- D. squarrosa* Schp. Wet places by the sides of small streams, etc., frequent.
- Blindia acuta* B. and S. Damp rocks, common.
- *var. *trichodes* Braithw. In similar situations to the last but less common; a curious form was found in a stream on Mullach Mor and in the Allt na h-Uamha.
- Dicranoweisia cirrata* Lindb. Walls and rocks, rare; Barkeval, Mullach Mor, and Kilmory.
- Campylopus Schwarzii* Schp. Peat bogs, rare; south side of Loch Scresort, and in Glen Shellesder.
- C. flexuosus* Brid. Chiefly on peaty banks in several localities.
- *var. *zonatus* Limpr. This variety was found on the north side of Loch Scresort, and on the moor to the south of Kinloch.
- C. pyriformis* Brid. Moorland and heaths, rather local.
- C. fragilis* B. and S. In similar situations to the last mentioned, but more widely distributed.
- C. Shawii* Wils. Found in a peat bog on the north side of Loch Scresort, thus providing another station for this rare endemic moss.
- C. setifolius* Wils. Only seen on the north side of Loch Scresort, and in the vicinity of Beinn nan Stac.
- C. atrovirens* De Not. Abundant everywhere in wet places.
- var. *falcatus* Braithw. This rare and attractive variety was only taken on the east side of Hallival.
- var. *muticus* Milde. Collected near Loch Bealach Mhic Neill.
- C. brevipilus* B. and S. Rare; Barkeval, Glen Shellesder, and Harris.
- **Dicranum fulvellum* Smith. Rock ledges; Black Hill, and Trallval at about 1000 feet.
- D. Bonjeani* De Not. Only seen near the sea on Monadh Dubh, and near Wreck Bay.
- D. scoparium* Hedw. In a variety of situations; frequent.
- *var. *orthophyllum* Brid. On boggy ground below the footpath east of Beinn nan Stac.

var. *spadiceum* Boul. Seems to be more frequent than the type.

D. majus Turn. Widely scattered, and reaching the summit cliffs of Askival.

D. fuscescens Turn. More lowland, and in drier situations than the last; occasional.

D. Scottianum Turn. Rare, usually not far from the sea; on both sides of Loch Scresort, and on rocky ledges near Allt an Rhudha and Kilmory Glen.

Leucobryum glaucum Schp. Moorlands, occasional.

**Fissidens viridulus* Wahl. Taken once in the plantation at Papadil.

F. bryoides Hedw. Shady places, Salisbury Dam and in the neighbourhood of Kinloch; rare.

F. osmundoides Hedw. Damp mountain slopes, frequent.

F. adiantoides Hedw. Wet rocks, frequent; occasionally in bogs.

F. decipiens De Not. Damp limestone rocks, and also rock crevices into which calcareous sand had drifted, frequent; also found on Hallival and Mullach Mor.

F. taxifolius Hedw. Of local occurrence in lowland shady situations.

Grimmia apocarpa Hedw. Rocks, frequent.

var. *rivularis* W. and M. On a rock at the margin of Loch Bealach Mhic Neill.

*var. *gracilis* W. and M. Recorded from Hallival, Fionchra, and Salisbury Dam.

G. maritima Smith. Maritime rocks, locally frequent; also away from the sea on Askival and Ruinsival.

G. funalis Schp. Rocks, Monadh Dubh, Black Hill, and Fionchra.

G. pulvinata Smith. Limestone rocks and on walls, rare.

**G. orbicularis* Bruch. Dry limestone rocks, Monadh Dubh, which station provides a considerable northern extension of its range in Britain.

G. trichophylla Grev. Rocks and walls, not uncommon; a fruiting specimen was collected on Hallival.

G. decipiens Lindb. Rarer than the last in similar situations.

G. patens B. and S. Rocks, very rare; Barkeval and Bloodstone Hill.

G. Doniana Sm. Collected only once from dry crevices of rocks on the lower slopes of Trallval above Loch Fiachanis.

G. ovata Schwaeg. Rare, on rocks; near Salisbury Dam, Glen Shellesder, and below An Dornabac.

Racomitrium ellipticum B. and S. Mountain rocks, frequent.

- R. aciculare* Brid. Rocks, frequent, especially at the lower elevations.
- R. protensum* Braun. Rocks, rare; south side of Loch Scresort, Hallival, and Mullach Mor.
- R. fasciculare* Brid. Common on rocks.
- R. heterostichum* Brid. Widely distributed on rocks, etc., common.
 var. *alopecurum* Huebn. Occasionally on the higher mountain rocks.
 var. *gracilescens* B. and S. Has only been noted from Hallival, Orval, and Ruinsival.
- **R. sudeticum* B. and S. Higher rocks, Barkeval, Askival, and Bloodstone Hill; also on Mullach Mor.
- R. lanuginosum* Brid. Generally abundant, and sometimes forming the dominant feature of the vegetation at the higher elevations.
- R. canescens* Brid. Stony heaths, roadsides, etc., common.
 var. *ericoides* B. and S. Has been recorded from Barkeval, Fionchra, and Ruinsival.
- Ptychomitrium polyphyllum* Fuern. Rocks, boulders, and walls; frequent.
- Glyphomitrium Daviesii* Brid. Local on rocks; the lower eastern slopes of Hallival, Kilmory, Long Loch, and Ruinsival above Loch Fiachanis.
- Hedwigia ciliata* Ehrh. Mountain rocks, frequent, and down to nearly sea level in places.
- Tortula muralis* Hedw. Walls, Kinloch and neighbourhood.
 *var. *rupestris* Schultz. Noted once in Kinloch Castle grounds.
- T. subulata* Hedw. Sandy ground and crumbling rocks; Kinloch, Kilmory, Fionchra, and Monadh Dubh.
- T. ruraliformis* Dixon. Blown maritime sand; abundant locally at Kilmory.
- Barbula rubella* Lindb. Rocks, walls, and banks, from sea level to nearly 2000 feet; not uncommon.
 *var. *ruberrima* Ferg. Much rarer than the species; wet rocks on the north side of Fionchra, Salisbury Dam, and Black Hill.
- B. tophacea* Mitt. Recorded only from Bloodstone Hill.
 var. *acutifolia* Schp. Again from Bloodstone Hill where it was found growing in a tuft with *Trichostomum crispulum* and *Bryum capillare*.
- **B. fallax* Hedw. Clay bank, Monadh Dubh. (Probably this, J. B. D.)
- **B. rigidula* Mitt. Rocks, frequent.

- B. cylindrica* Schp. Rare and local; cliffs north face Fionchra, Bloodstone Hill, and on the dunes Samhnán Insir.
- B. convoluta* Hedw. Recorded from Kinloch Castle grounds, Kilmory, and Samhnán Insir.
- **B. unguiculata* Hedw. Very local; only on sandy ground at Kilmory.
- **Leptodontium recurvifolium* Lindb. One station only, on the western summit cliffs of Askival.
- Weisia microstoma* C. M. Three records; bank of turfy mound, Salisbury Dam, moor near An Dornabac, and Bloodstone Hill.
- **W. crispata* C. M. On cliff ledges, south side of Fionchra, Salisbury Dam, and east of Harris.
- W. viridula* Hedw. Dry banks, frequent.
- **W. tenuis* C. M. One record only, from sandy ground on the bank of the stream above Salisbury Dam, providing a considerable northern extension of its range in Britain.
- **W. calcarea* C. M. var. *viridula* C. M. Collected twice only, on Ruinsival and Salisbury Dam. Appears to be found elsewhere in Scotland only in v.c. 91.
- W. rupestris* C. M. Wet rocks, usually limy, rare.
- W. curvirostris* C. M. Calcareous rocks, Kilmory, Monadh Dubh, and Bloodstone Hill.
- *var. *commutata* Dixon. One record from Barkeval.
- *var. *insignis* Dixon. This very rare form was collected in a rocky gorge of the Kilmory River just below the bridge on the Kilmory Road.
- *var. *catractarum* Schp. New to Britain; on a wet limestone cliff near a waterfall on the coast, Monadh Dubh.
- W. verticillata* Brid. Calcareous rocks, Monadh Dubh.
- Trichostomum crispulum* Bruch. On calcareous rocks and sand, and mortared walls; occasional.
- T. mutabile* Bruch. Rocks, etc., frequent.
- var. *littorale* Dixon. Usually near the sea in similar situations to the last, but sometimes at an elevation of 1000 feet or more; not uncommon.
- T. tenuirostre* Lindb. Seen only once on wet rocks on the lower slopes of Ainshval.
- **T. hibernicum* Dixon. This rare British moss is widely distributed on Rhum in suitable habitats.
- T. tortuosum* Dixon. Rocks, generally frequent, and becoming locally abundant in the limestone area.
- *var. *fragilifolium* Dixon. Taken once on Meall Breac.

- Encalypta ciliata* Hoffm. Rock crevices, local; Fionchra and Bloodstone Hill.
- **E. rhabdocarpa* Schwaeg. Only on the bridge over the Kinloch River.
- E. streptocarpa* Hedw. Crevices of limestone rocks, Monadh Dubh, and limed wall of ruined house, Samhnan Insir.
- Anoetangium compactum* Schwaeg. Shady rock crevices, frequent.
- *var. *pellucidum* Dixon. Collected twice, on wet rocks beside a stream north-east of Fionchra, and in a similar situation on the western lower slopes of Trallval.
- Zygodon lapponicus* B. and S. Clefts of rocks, Bloodstone Hill, Black Hill, Ainshval, and near the Long Loch.
- Z. Mougeotii* B. and S. Damp mountain rocks, reaching the summit cliffs of Askival, frequent. In fruit on Fionchra and Black Hill.
- **Z. viridissimus* R. Brown var. *rupestris* Hartm. On rocks, Hallival, and near the lime kiln, Kinloch.
- **Z. Stirtoni* Schp. One record from a rock in Glen Kinloch.
- **Ulota Drummondii* Brid. On a Spruce, Kinloch.
- U. Bruchii* Hornsch. Seen twice only, on a low bush on the south side of Mullach Mor, and on a Rowan tree on the north side of the same hill.
- **U. crispa* Brid. Collected on a tree at Kinloch, and on the same Rowan as above on Mullach Mor.
- var. *intermedia* Braithw. Trees, including a Bamboo; abundant Kinloch, rare elsewhere.
- U. phyllantha* Brid. Very abundant on trees especially at Kinloch; also occasionally on rocks at low levels all over the island.
- U. Hutchinsiae* Hamm. Not uncommon on rocks all over the island, but not seen above 1000 feet.
- Orthotrichum rupestre* Schleich. In similar situations to the last but rarer.
- O. anomalum* Hedw. var. *saxatile* Milde. Rocks and walls, rather rare; Kinloch and neighbourhood, Ruinsival, Papadil, and Monadh Dubh.
- O. affine* Schrad. Taken twice; on a rock at Kilmory, and on a Pear tree in Kinloch kitchen garden.
- **O. pulchellum* Smith. Occasionally on trees in Kinloch Castle grounds (once on a Bamboo); found once elsewhere on *Salix Arbuscula* in its only station on Fionchra.
- Oedipodium Griffithianum* Schwaeg. Very rare on rock ledges; cliffs above Black Hill Loch, and lower slopes of Ainshval.

- **Splachnum ampullaceum* L. Only in two localities, Kinloch and south-east of Papadil.
- S. sphaericum* Linn. fil. Again only two records; bog at the top of Glen Shellesder, and on moorland near Loch a' Ghille Reamhra.
- Tetraplodon mnoides* B. and S. More frequent than the last two, occurring here and there on most of the higher hills. Found on a feather on Barkeval.
- Funaria ericetorum* Dixon. Not uncommon on peaty banks, Monadh Dubh, gorge Camas na h-Atha, Glen Shellesder, and banks of stream running north from the Long Loch.
- F. Templetoni* Sm. Shady, steep peaty banks and vertical rocks, frequent.
- F. hygrometrica* Sibth. In several scattered places and reaching the summit cliffs of Askival.
- Aulacomnium palustre* Schwaeg. Bogs and wet heaths, not infrequent, and mostly below 1000 feet.
- **Bartramia ithyphylla* Brid. Mountain rocks, not uncommon.
- B. pomiformis* Hedw. Clefts of lowland rocks, less frequent than the last.
- Philonotis fontana* Brid. Wet peaty places beside streamlets, etc.; common and very variable.
- P. capillaris* Lindb. Of local occurrence usually on mountain rocks; summit cliffs of Askival, Bloodstone Hill, Fionchra, Ainshval, and Salisbury Dam.
- Breutelia arcuata* Schp. Moist peaty ground and damp rocks, common; found in fruit on Barkeval.
- **Webera polymorpha* Schp. Only record from the summit cliffs of Askival. (Think correct, J. B. D.)
- W. acuminata* Schp. Collected at Kinloch, and on a wet rock ledge below the summit of Sgurr nan Gilleann.
- W. elongata* Schwaeg. Mountain rocks and banks, occasional.
- W. cruda* Schwaeg. On rocks, occasional; Hallival, north side of Fionchra, Bloodstone Hill, and the limestone, Monadh Dubh.
- W. nutans* Hedw. Peaty and sandy soils, frequent, reaching the summit cliffs of Askival.
- **W. annotina* Schwaeg. One record only, from sandy peaty bank above Salisbury Dam.
- *var. *erecta* Correns. Sandy bank, Trallval, and shaded rocks, Salisbury Dam.
- **W. prolifera* Bryhn. In similar situations to the last, Salisbury Dam, west side of Hallival, and banks of stream running north from the Long Loch.

- **W. commutata* Schp. From one station only, on the summit cliffs of Askival.
- **W. albicans* Schp. Damp banks by streams, rather rare.
- **Plagiobryum Zierii* Lindb. Clefts and ledges of rocks, local; Barkeval, Meall Breac, north and south sides of Fionchra, Black Hill, and Sgurr nan Gilleán.
- Bryum filiforme* Dicks. Quite frequent on wet rocks.
- **B. concinnatum* Spruce. This rare moss was found in 1943 in good condition near Salisbury Dam, and was collected again in 1944 in the same area.
- B. inclinatum* Bland. The only definite localities are the sand dunes near Samhnan Insir, and Kinloch Castle kitchen garden.
- B. pallens* Sw. Common in wet places and reaching the summit cliffs of Askival.
- **B. turbinatum* Schwaeg. Another rare British moss which was found in 1943 at Salisbury Dam, and collected again in 1944.
- B. pseudo-triquetrum* Schwaeg. Wet places, frequent.
- B. caespiticium* L. One record from an ash heap at Kinloch.
- B. capillare* L. Walls, rocks, etc., frequent.
- **B. atropurpureum* W. and M. Dry and sandy ground, rather rare; Kinloch, Monadh Dubh, near Loch Fiachanis, and Samhnan Insir.
- B. alpinum* Huds. Wet rocks, especially near the sea, rather frequent. Where it occurs away from the coast on the hills, it is almost entirely green in colour.
- B. argenteum* L. Paths, sandy ground, etc., rare; Kinloch and Samhnan Insir.
- *var. *lanatum* B. and S. Unfixed sand dunes, Kilmory.
- **B. roseum* Schreb. West side of Bloodstone Hill, very dwarfed on account of its exposed position; an interesting extension of its range in Britain.
- **Mnium affine* Bland. On grassy banks; Kinloch River near its mouth, and Salisbury Dam.
- *var. *elatum* B. and S. Marshy ground in a pasture field at Kinloch.
- **M. rostratum* Schrad. Sandy grassy banks, Fionchra; also probably in Glen Kinloch, but specimen too poor for certain identification.
- M. undulatum* L. Grassy places, frequent; collected in fruit in Kinloch Castle grounds.
- M. hornum* L. In a variety of habitats, common.

- **M. stellare* Reich. Shady rock ledges, twice only; Bloodstone Hill and north side of Fionchra.
- M. punctatum* L. Damp rocky situations, frequent.
- *var. *elatum* Schp. Glen Kilmory.
- Fontinalis antipyretica* L. On rocks and stones in streams, frequent, and often locally very abundant.
- *var. *gracilis* Schp. Found only in a stream north-east of Hallival.
- Cryphaea heteromalla* Mohr. On two trees in sheltered positions in grounds of Kinloch Castle.
- Neckera crispa* Hedw. Rather common on limestone rocks, Monadh Dubh, but also recorded from Fionchra, Bloodstone Hill, and cliffs east of Harris.
- var. *falcata* Boul. This variety or form was collected on the limestone, and also on Orval.
- N. complanata* Huebn. Again on the limestone, Monadh Dubh, and at Kilmory on rocks on to which calcareous sand had drifted.
- Pterygophyllum lucens* Brid. In sheltered hollows among rocks, not uncommon.
- Pterogonium gracile* Swartz. Not uncommon on cliff ledges, Fionchra, and recorded elsewhere only from a gully on the south-west side of Barkeval.
- Antitrichia curtipendula* Brid. Locally abundant on rocks, Fionchra, but rare on Orval, Bloodstone Hill, and Ruinsival above Loch Fiachanis.
- Porotrichum alopecurum* Mitt. Not uncommon but very variable; in sheltered localities often luxuriant, but in the open where it occurs in association with other mosses, usually very dwarfed.
- Heterocladium heteropterum* B. and S. Occasional in sheltered positions but reaching the summit cliffs of Askival; again often mixed with other mosses.
- Thuidium tamariscinum* B. and S. Generally very abundant and sometimes fruiting.
- T. delicatulum* Mitt. On grassy slopes from sea level to the summit cliffs of Askival; occasional.
- Climacium dendroides* Web. and Mohr. In sandy turf on the sand dunes, Samhnan Insir.
- **Cylindrothecium concinnum* Schp. Collected once from the fixed sand dunes at Samhnan Insir.

- Myurium hebridarum* Schp. This interesting moss was observed only once, at the unusually high elevation of 1600 feet, below the cliffs on the east side of Orval overlooking Loch a' Ghille Reamhra.
- Orthothecium rufescens* B. and S. Moist crevices of the limestone rocks on Monadh Dubh, where it is not rare.
- O. intricatum* B. and S. Collected only once on Barkeval.
- Camptothecium sericeum* Kindb. Rocks, not uncommon, but not seen on any of the higher hills.
- C. lutescens* B. and S. Sand dunes at Kilmory and Samhnan Insir, rather rare.
- **Brachythecium glareosum* B. and S. Found once in the turf of the fixed sand dunes at Samhnan Insir.
- B. albicans* B. and S. The only record is for the unfixed dunes at Kilmory.
- B. rutabulum* B. and S. In a variety of situations, frequent.
- B. rivulare* B. and S. Wet rocks, etc., just about as frequent as the last.
- **B. velutinum* B. and S. On the trunk of a Rowan, Kinloch.
- B. populeum* B. and S. Rocks, etc., two records from Kinloch and Papadil.
- B. plumosum* B. and S. Rather common on rocks by streams, and reaching the summit cliffs of Askival.
- B. purum* Dixon. Among grass, etc., common.
- Hycomium flagellare* B. and S. Wet rocks, occasional.
- **Eurhynchium piliferum* B. and S. Shady rock ledges, north side of Fionchra, and Trallval.
- E. praelongum* Hobk. A common species preferring shade at the lower elevations.
- *var. *Stokesii* Brid. In a gorge north-east of Fionchra.
- E. Swartzii* Hobk. In sheltered places, not rare, and fruiting in the grounds of Kinloch Castle.
- E. pumilum* Schp. Another of the species not seen by the authors, but found by Marquand and listed by Blackburn and Lobleby.
- E. myosuroides* Schp. Generally abundant on rocks, boulders, and trees.
- var. *brachythecioides* Dixon. On rocks, frequent.
- E. myurum* Dixon. Rather rare; on rocks, boulders, etc., especially when they contain lime.
- E. striatum* B. and S. A lowland species, often among grass; occasional.
- E. rusciforme* Milde. Locally abundant in some of the streams.

E. confertum Milde. Only collected at Kinloch.

Plagiothecium elegans Sull. Woods in the Kinloch area and at Papadil, but occurring also on rocks, Mullach Mor, Ainshval, and summit cliffs of Askival.

**P. Muellerianum* Schp. Found only on Orval; an exceptionally interesting find in view of its rarity in Britain.

P. pulchellum B. and S. Crevices of rocks, Allt na h-Uamha, Barkeval, Fionchra, Black Hill, and Ruinsival.

P. denticulatum B. and S. Favours sheltered situations, and reaching the summit cliffs of Askival.

**P. silvaticum* B. and S. Rocks close to the sea at Guirdil, and probably also in the gorge on the north-east side of Fionchra.

P. undulatum B. and S. Under heather, etc., frequent.

Amblystegium serpens B. and S. Mostly on stones, rare; Kinloch Castle grounds and neighbourhood, and Papadil.

A. filicinum De Not. Wet ground often calcareous, chiefly in the northern part of the island, but recorded elsewhere from Harris and Ainshval.

*var. *trichodes* Brid. Sheltered rock ledge in cave on the shore below Bloodstone Hill.

Hypnum riparium L. On the base of a tree trunk, Kinloch.

**H. elodes* Spruce. Only one record from Kinloch.

H. stellatum Schreb. Marshes and bogs, not infrequent, and sometimes in fruit.

*var. *protensum* Roehl. Collected once on Meall Breac.

**H. Sendtneri* Schp. Marshy ground on south side of Mullach Mor.

H. fluitans L. In dried-up muddy pools, Kilmory Glen, and recorded from Mullach Mor by Blackburn and Lobley.

H. exannulatum Gumb. Very wet ground on the south side of Loch Scresort, and in Glens Kinloch, Kilmory, and Shellesder.

**H. uncinatum* Hedw. Only two records from the summit cliffs of Askival and from Ruinsival.

**H. vernicosum* Lindb. One station only, in a bog near the right bank of the Kinloch River about half a mile from its mouth.

H. revolvens Swartz. Bogs, etc., rather frequent.

H. intermedium Lindb. Again only one record, Glen Kinloch.

H. commutatum Hedw. Usually on very wet ground or on dripping rocks at rather low elevations; frequent.

H. falcatum Brid. In similar situations, north side of Loch Scresort, Mullach Mor, Glen Shellesder, and on the limestone area of Monadh Dubh.

*var. *gracilescens* Schp. Monadh Dubh.

- H. cupressiforme* L. In a variety of habitats, common.
 var. *resupinatum* Schp. Kinloch and neighbourhood, and Kilmory.
 var. *filiforme* Brid. On tree trunks south side of Loch Scresort, and wood, Kinloch.
 var. *ericetorum* B. and S. Heathy places, occasional.
 var. *tectorum* Brid. Rocks, Kilmory, and near the lime-kiln, Kinloch.
 *var. *elatum* B. and S. Calcareous ground, Monadh Dubh.
- H. hamulosum* B. and S. Observed in two localities, lower slopes of Barkeval and on grassy slopes of Fionchra.
- H. callichroum* Brid. On rocks from near sea level at Kilmory to the summit of Barkeval; occasional.
- H. molluscum* Hedw. Abundant in a variety of situations.
 var. *condensatum* Schp. Found by Marquand and recorded by Blackburn and Lobley, but not seen by the authors.
 *var. *robustum* Boul. This rare mountain form was collected from a wet rock ledge in the corrie below the summit of Sgurr nan Gilleann.
- *var. *fastigiatum* Bosw. Only found at Kilmory.
- H. palustre* Huds. Stones and rocks by streams, Hallival, and waterfall north-east of Fionchra.
- H. scorpioides* L. Very wet peat, often under water, not uncommon.
- H. trifarium* W. and M. In similar situations, but found only once in Glen Kinloch.
- H. sarmentosum* Wahl. In bogs and beside small streams, rare; Mullach Mor and Monadh Dubh.
 var. *fallaciosum* Milde. Monadh Dubh.
- H. cuspidatum* L. In wet places, frequent.
- H. Schreberi* Willd. Rather common under heather, etc.
- Hylocomium splendens* B. and S. In heathy situations, abundant.
- H. brevirostre* B. and S. Grassy shaded banks, rare; Fionchra and Kilmory.
- H. loreum* B. and S. Common on rock ledges and peaty soil.
- H. squarrosus* B. and S. Grassy banks, etc., and reaching the summit cliffs of Askival; very common.
 var. *calvescens* Hobkirk. One patch in Kinloch Wood.
- H. triquetrum* B. and S. Usually among grass in drier situations than the last species, occasional. Found in fruit on Fionchra.

ADDENDUM.

Since the above paper was written, a further visit to Rhum has been made, with the result that the following 15 species and varieties, of which 11 are new to v.c. 104, have been added to our list. The total number of species and varieties from Rhum has thus been increased to 292 and the number of new Vice-County records to 90.

**Tetraphis Browniana* Grev. Western summit cliffs of Askival, at the unusually high altitude of about 2300 feet.

Pleuridium axillare Lindb. On glacial drift, Glen Duian.

**Rhabdoweisia crenulata* Jameson. In gorge of stream running into the sea east of Creag na h-Iolaire.

Campylopus brevipilus B. and S. var. *auriculatus* Ferg. Glen Duian.

**Dicranum uncinatum* C. M. In the same gully as *Rhabdoweisia crenulata*.

Barbula revoluta Brid. On a bridge over the Kinloch River at Kinloch.

**Leptodontium flexifolium* Hampe forma *alpina* Dixon. Growing in a lax tuft of *Zygodon Mougeotii* collected from wet cliffs on the north side of the coll between Askival and Trallval. Mr. Duncan states that our plant is identical with material collected from Ben Lawers and Creag an Lochain by Mr. H. H. Knight in 1909 and originally named by him and Mr. W. E. Nicholson *Barbula rubella* var. *dentata* Schp. (Moss Exchange Club Report, 1910) but subsequently corrected to *Leptodontium flexifolium* forma *alpina* by Dixon in 1910. Mr. Duncan can, however, find no reference in the literature at his disposal to this form, nor does it appear in the latest edition of Dixon's "Students Handbook of British Mosses", though in his footnote to *L. flexifolium* reference is made to a curious reddish form which may be the plant in question. Until the matter can be further investigated it has been decided to retain Dixon's name for the Rhum specimen.

**Trichostomum flavovirens* Bruch. Sea cliffs near the shore, Wreck Bay.

**Leptobryum pyriforme* Wils. On wet ground at the base of cliffs, south side Loch Scresort.

Fontinalis squamosa L. On rocks in stream, Glen Duian.

- **Heterocladium Macounii* Best. This interesting moss was collected from a vertical face of a shaded gully on the northern lower slopes of Fionchra. Although Mr. Duncan considers this to be a rather doubtful species, he informs us that the Rhum plant is the most satisfactory of the specimens so far examined by him from four or five localities in Britain.
- **Eurhynchium rusciforme* Milde var. *alopecuroides* Brid. In the stream, Glen Duian.
- **Amblystegium curvicaule* Lindb. At about 850 feet in Glen Duian. This seems an unusually low altitude for a species previously reported only in Britain from the summit cliffs of Ben Lawers.
- **Hypnum Patientiae* Lindb. Wet pasture field, Kinloch.
- **H. ochraceum* Turn. On a rock in the stream, Glen Guirdil, and also in a stream north of Fionchra.

NOTEWORTHY SEDGES FROM THE INNER AND OUTER HEBRIDES,
WITH AN ACCOUNT OF TWO SPECIES NEW TO THE BRITISH
ISLES. By J. W. HESLOP HARRISON, D.Sc., F.R.S., F.R.S.E.

(Read 14th June 1945.)

During the past six years we have continued our investigations in the Flora and Fauna of the Scottish Western Isles, and no group has yielded more satisfactory results than the genus *Carex*. Unfortunately, however, several important forms have been encountered in very limited areas, and in exceedingly small quantity—facts that have necessitated delays in publication in order to carry out further explorations designed to determine, if possible, the full ranges of the species concerned in our area. During this enforced delay, the specimens in question have been placed on exhibition for the benefit of local societies; this fact has opened the door for their discussion by unauthorized persons who have never even seen the forms they purport to discuss. As this seems a highly reprehensible practice, and one likely to end in confusion, the present paper is written to supply botanists with reliable and authentic information about our plants, based upon the actual specimens in our possession.

Carex capitata L., Syst. Nat. Ed., 10, ii, p. 1261 (1759).

Densely caespitose. Rootstock brown, creeping, stoloniferous. Culm upright, setaceous yet rigid, triangular in section, 2–16 cm. high. Leaves rigid, channelled, setaceous, tips scabrous, half the length of the culm. Spikelet single, somewhat globose, about the size of a pea, dull yellow in colour, terminal half male, lanceolate; basal portion female; in fruit, more swollen and globular. Stigmas 2. Bracts, *when present*, leaflike, half as long again as the spikelet. Fruits densely imbricate, broadly ovate, flattish, without nervure, somewhat convex on the back, very smooth, shining, longer than the glumes. Glumes roundish, margins hyaline, otherwise chestnut brown. The species was placed by Fries amongst his *Pulicares*.

By a very curious coincidence, our experiences in respect to the occurrence of this plant in the Isle of South Uist (v.c. 110) paralleled exactly those described by Polunin in his "Botany of the Canadian Eastern Arctic" in discussing his discovery of the species in Eastern Baffin Land. He relates how he detected a characteristic tuft growing on a gentle slope of bare clay near the coast; we came across

a similar tuft on a bare stretch of soil lying at the head of two parallel slopes not far from the sea in the Truirebheinn area, north of Loch Boisdale in South Uist.

Generally speaking, *Carex capitata* is circumboreal in its distribution, with subarctic and alpine preferences. It reaches its most northerly station at a latitude of $72^{\circ} 42'$ north in Greenland, but is found from New Hampshire and Labrador westward to Alaska and passes down the Rocky Mountains to Mexico (20° north). In South America, it occurs in the Southern Andes and Tierra del Fuego. Its European distribution is northern and alpine, whilst in Asia its known stations are of much the same type.

Carex rupestris All.

Of sparse occurrence amongst the rocks just below the ridge on the northern slopes of Beinn Mhor, South Uist (v.c. 110).

Carex pauciflora Lightfoot.

Exceedingly local, although plentiful where it does occur, on very damp grassy places around Lochs Storab and Meall Daimh on Raasay (v.c. 104), and much rarer on similar ground between Sheaval and Trinival, South Uist (v.c. 110).

Carex microglochin Wahl.

Collected by Dr. W. A. Clark, just below the summit of Uisgnaval More, North Harris (v.c. 110), on a somewhat bare and damp patch of ground at an elevation of some 2000 feet, associated with *Luzula spicata*, *Festuca* spp., *Agrostis canina*, *Alchemilla alpina*, and *Euphrasia* sp.

This discovery supplies a welcome extension to the range of a recently discovered British species.

Carex maritima Gunn. Fl. Norv., ii, p. 131 (1772).

On dry sandy places on the western shore of South Harris (v.c. 110) where it is rare on the Traigh Scarasta, but quite plentiful on the Traigh an Taoibh Thuath; also frequent in certain damp hollows on the machair on the Isle of Berneray (Harris). This is, of course, the plant long familiar to us under the name of *Carex incurva* Lightfoot.

Carex chordorrhiza Ehrh.

In very small quantity on a patch of extremely boggy ground near Loch Stioclett, South Harris (v.c. 110); nevertheless, a useful increase in the range of a very local British plant hitherto only known from Sutherland. Attempts have been made to cultivate it but, although it has sent out stolons at least two feet long, it fails to flourish under artificial conditions.

Carex disticha Huds.

Locally plentiful on marshy ground fringing the loch near Cornaigmore in the north-west of the Isle of Tiree (v.c. 103).

Carex diandra Schrank.

Only observed by us around a tiny lochan near the Dun Beag, Miodar, in the extreme north-east of the Isle of Tiree (v.c. 103).

Carex paniculata L.

In great abundance in a flat boggy expanse in the centre of the Isle of Muck (v.c. 104) and in a marsh at the south end of Loch Bhasapoll, Isle of Tiree (v.c. 103); in the Outer Hebrides it appears equally plentiful in a marsh near Nunton and beside the north-west shores of Loch na Liana Moire, Isle of Benbecula (v.c. 110), but is less common in similar habitats on the Isle of Baleshare, North Uist (v.c. 110).

Carex Pairaei F. Schultz.

Rare, north-west of Heishval as one approaches Traigh Varlish, Isle of Vatersay (v.c. 110); apparently the second Scottish station.

Carex curta Good.

Found only in a shallow ravine or gorge, north-west of the ruins on the Isle of Pabbay, Barra Isles (v.c. 110).

Carex bipartita All., Fl. Pedem., ii, p. 265 (1785).

Although the names *Carex Lachenalii* Schkuhr and *C. lagopina* Wahl. have been, until recently, in use for this species in Britain, for reasons supplied by Mackenzie, the name *Carex bipartita* All. is now adopted. The plant was collected on damp ground between the stream in the Coire Serien and the crags on Sgaoth Ard, North Harris (v.c. 110). This species has now been kept alive since 1941, but it has proved a very difficult subject!

Carex Halleri Gunn.

First discovered by Dr. W. A. Clark on grassy areas on the summit cliffs of Eaval, Isle of North Uist (v.c. 110); later it has been collected on the South Lee on the same island, and on the southern approaches of Beinn Mhor, South Uist, as one climbs *viâ* the Allt Volagir; detected likewise in small numbers on damp ground on the Chapán Breac, Isle of Rhum (v.c. 104). Hebridean examples vary in height from 3–12 cm.

Carex atrata L.

Scattered irregularly, and very sparingly, in tumbled grassy places along the burn on the slopes of Barkeval, Isle of Rhum (v.c. 104), occurring at quite low altitudes. In addition to more or less

typical examples, specimens appertaining to the var. *gelida* Sch. were also collected. Whilst the species itself is new to v.c. 104, the variety is now recorded for the first time from the British Isles.

Carex Hudsonii Ar. Benn.

Another of Dr. W. A. Clark's discoveries; first noted by him on moorland ground near the pièr, Isle of Great Bernera, off the west coast of Lewis (v.c. 110), and, subsequently, around Loch Bhasapoll, Isle of Tiree (v.c. 103).

Carex Bigelowii Torrey ex Schwein. in Ann. Lyc., New York, i, p. 67 (1824).

This is, of course, the plant usually known as *Carex rigida* Good. to British botanists. As this name was rendered invalid by an earlier homonym, Druce, in the Comital Flora, employed, quite mistakenly as it has turned out, the name *Carex concolor* R. Br. now, by consent, abandoned in favour of *Carex Bigelowii* Torrey.

The species grows at various altitudes in the islands, from about 100 feet on the Isle of Coll (v.c. 103), 800 feet near Dun Caan, Raasay (v.c. 104), 900 feet on Eaval, North Uist (v.c. 110), and 1500–2000 feet on Rhum (v.c. 104), South Uist and Harris (v.c. 110).

Carex juncella Th. Fr.

This sedge, sometimes treated as a form of *Carex Goodenowii* Gay, is thinly distributed in Great Bernera (Lewis), on the Isle of Scotasay (Harris), and in Beesdale (South Harris); all in v.c. 110. It is described as "*culmo elongato gracile, foliis convoluto-filiformibus spicis subdistantibus tenuioribus*" and is reported by Andersson as the sole form occurring in Lapland and the Arctic regions.

Carex magellanica Lam.

Reported previously, but apparently with considerable doubt, from the Outer Hebrides; now recorded with certainty from a bog near the South Lee, Isle of North Uist (v.c. 110).

Carex rariflora Sm.

Collected from a very small colony growing in wet ground along the margin of a runnel flowing amongst the rocks on the northern slopes of Beinn Mhor, Isle of South Uist (v.c. 110). Grows fairly well, but fails to flower in cultivation.

Carex glacialis Mackenzie in Bulletin Torrey Bot. Club, xxxvii, p. 244 (1910).

Root caespitose. Culm 3–8 cm. high, rigid, upright, smooth and only obscurely triangular, surrounded at the base by many leaves. Leaves, toward their bases, keeled, but solid and triangular

terminally, stiff, rough and dry in texture, curved outward, dark green in colour; outer leaves often persistent and withered. Lower sheaths brownish, rarely purple.

Lower bract subtruncate, somewhat amplicant, with a hyaline margin and a foliaceous hirtellous blade; upper bract fuscous scarious, submucronate.

Terminal spikelet male, female spikelets lax, two (rarely three) in number, upright, approximated, few-flowered (3-6), subsessile, or, especially the lower spikelet, shortly stalked. Glumes fuscous, with a paler nerve, and the margins whitish scarious. Perigynia broadly ovoid, grayish-fuscous, 2 mm. long, smooth, beak short, orifice oblique. Stigmas 3. Placed by Fries amongst his *Frigidae*.

This species was discovered on dry stony ground on the upper slopes of the southern turning of the Barkeval ridge, Isle of Rhum (v.c. 104). General distribution abroad: circumpolar, with its southern limits Alaska, Newfoundland, Iceland, and Scandinavia.

The Rhum plants differ in several respects from the descriptions provided by various authors. Kükenthal, for instance, refers to the basal sheaths as "*vaginae inferiores purpureae*," whilst Andersson applies the term "*purpurascentes*" to them; similarly, whilst admitting that his *Carex terrae-novae* occasionally develops slightly purplish sheaths, Fernald uses their pale brown coloration to differentiate the species. All that can be said of the few British specimens subjected to examination is that most are brown. Again, Blytt makes the leaves "*naesten traadsmale*," and Andersson at one point indicates that they are "*involuta-filiformes*" and at another that they appear "*angustissimi*"; some leaves of the plants in my possession attain a breadth of 1.6 mm. Finally, Blytt says that their colour is "*blaagrønne*"; as set out above, the leaves of the Rhum plants are, without exception, dark green.

As will have been observed, we have used the name *Carex glacialis* Mackenzie for the species long known as *Carex pedata* Wahl. This is unavoidable because of the previous use of the same name by Linnaeus for a plant of uncertain position. The untenability of Wahlenberg's name was first pointed out by Simmons in 1906, and Mackenzie remedied matters just four years later by putting forward the name now employed.

Carex bicolor All.

Since its original discovery in 1941 we have observed this plant each year except in 1944. However, in addition to forms we regard as typical, there occur regularly others which seem worthy of a name: *C. bicolor* var. *microcarpa* var. nov., spica pisi magnitudine; fructibus

parvis; foliis longioribus et tenuioribus. Barkeval, Isle of Rhum (J. W. Heslop Harrison-type).

Carex caryophyllea Latour.

Sporadically distributed in Raasay, Scalpay, and in the Small Isles Parish (v.c. 104), Coll and Tiree (v.c. 103), but rarer in the Isles of Vatersay and Pabbay (v.c. 110).

Carex vaginata Tausch.

First collected by my colleague Dr. K. B. Blackburn in the Coire Dubh on a flat, damp, grassy stretch north-west of the stream Abhainn Gheatry as it leaves Beinn Mhor, Isle of South Uist (v.c. 110).

Carex atrofusca Schkuhr.

Very rare on boggy ground on the southern turning of the Orval-Ard Nev ridge, Isle of Rhum (v.c. 104).

Carex capillaris L.

On the same slope as the preceding, but near the Sron an t'Saighdeir, Isle of Rhum (v.c. 104).

Carex lepidocarpa Tausch.

Sparingly on Coll and Tiree (v.c. 103), but more frequent in the Outer Isles from Lewis to Vatersay (v.c. 110); not, however, noted in the Isle of Barra.

Carex distans L.

Not rare in the Outer Isles (v.c. 110), nor in Coll and Tiree (v.c. 103), but not really common in v.c. 104. It, however, may be found near Loch Balachuinn, Raasay, and in Southern Scalpay. It was also collected on the Hyskeir reef in 1938, and two years ago near Cave Bay, Isle of Rhum.

Carex lasiocarpa Ehrh.

Plentiful on the shores of lochs in the Loch a'Mhill Aird area on Coll (v.c. 103) and on a lochan, north of Crogary Beg, Isle of North Uist (v.c. 110).

Carex acutiformis Ehrh.

Discovered on the Isle of Baleshare, west of the Isle of North Uist (v.c. 110). Perhaps it is as well to make it clear here that the species has been collected by Capt. J. Heslop Harrison in the Orkney Islands (v.c. 111) where it also seems to be a new county record.

Carex vesicaria L.

Of infrequent occurrence on the Isles of Raasay, Rhum, Eigg, and Muck (v.c. 104) and about lochs near Howmore, Isle of South Uist (v.c. 110).

Carex rostrata Stokes $\times$ *C. vesicaria* L.

Although we have not yet detected the pure species *C. vesicaria* in the Isle of Harris, this hybrid, determined by Mr. E. Nelmes, was noted around lochans in the Langracliett and Nisabost areas, South Harris (v.c. 110).

Carex brunnea R. Br.

This sedge known from Japan *viâ* the East Indies to Mauritius was found flourishing in the Kinloch grounds, Isle of Rhum, where it had almost certainly been introduced with bamboos or similar plants; the form encountered was var. *minor* Boott. Named by Mr. E. Nelmes who has so kindly checked our determinations in this group.

CONCLUDING REMARKS.

The list given does not, of course, purport to contain the whole of the sedge flora of the Scottish Western Isles. It includes only those species that are new to the British Isles, or to the Hebrides, with some account of those which, on account of their rarity, or some other special reason, seem worthy of discussion.

Broadly speaking, they break into two groups: (1) species of Arctic or Alpine proclivities and (2) those which, whilst possessing individual ecological requirements, are of fairly general distribution in the British Islands. Of these two sections, the first appears to be by far the more important, as not only does it comprise within its limits several species new to the British Flora but, in addition, supplies new stations for forms which, up to the present, have been regarded as being amongst the rarest and most local of our native plants.

The latter observation brings us to other remarkable features which characterize the distribution and occurrence of these, as well as of other, Arctic-Alpine plants in the Hebrides. The most striking of these are displayed in their erratic distributions, the fewness of their habitats, their presence in exceedingly small quantity and the almost total failure of stations for any one plant to coincide with, or even approximate to, those of another. In point of fact, *Carex Halleri* alone has been found in more than one island, and it, strangely enough, has been collected in three stations in the outer Isles, and in one in the Isle of Rhum; moreover, its Rhum locality lies just a short distance to the east of that in which *Carex bicolor* grows.

To my mind, these peculiarities all lead unmistakably to the conclusion that the plants concerned form the impoverished remnants

of an old flora. Furthermore, the longer our studies have proceeded, the more we have had it impressed upon us that this impoverishment is still progressing. In spite of this, we are firmly convinced that the retrogression of the island floras was initiated by, and therefore dates back to, the last great climatic deterioration which commenced about the year 750 B.C. This inaugurated a wetter and cooler epoch, leading to the development of peatbogs and a general intensification of moss growth. As a natural consequence, the old Hebridean forests vanished save for small isolated fragments, and movements in the way of solifluction were set up which, as the years passed, have swept away many irreplaceable elements of the upland floras of the islands. This process has, undoubtedly, for a long period of years, been aided by human activities, but recently we have observed it expedited, more especially on the Isle of Rhum, where the superimposition of a heavy sheep population on an island, already well stocked with deer and wild goats, has already had marked effects on soil stability, especially on the Barkeval slopes. However, as these topics will be dealt with at some length in a forthcoming paper on the History and Geography of the Flora and Fauna of the Inner and Outer Hebrides, it is not proposed to give a detailed consideration of the various problems raised here.

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TRANSACTIONS
OF THE
BOTANICAL SOCIETY OF EDINBURGH

SESSION CX

OBSERVATIONS ON THE MOSSES OF TORRIDON, WESTER ROSS.
By E. V. WATSON, B.Sc., Ph.D.

(Read 16th May 1946.)

The vice-county 105, in which Torridon is situated, is one that has not been studied very fully from the bryological standpoint, a fact which is made quite clear by reference to the "Census Catalogue of British Mosses" (2), for absent from the records there given are numerous species which a careful search would undoubtedly reveal in the fairly rich terrain of Wester Ross.

The plan of the present short paper is twofold: (1) to place on record a list of those mosses found and identified in the course of a few days spent in the Torridon district in September 1944, and (2) to draw attention to the ecological part played by certain mosses in the vegetation of moorland and mountain-side in the vicinity of Torridon and, when possible, to suggest groups of moss species which comprise distinct and noteworthy bryophytic communities in themselves.

Concerning the first of these objectives, it is hardly necessary to point out the fact of the extreme incompleteness of such a list as this. In no sense is it intended to imply that species absent from this list are not to be found in the country around Torridon. Numerous species are new vice-county records; but the only one of these of outstanding interest is *Campylopus Shawii*.

Campylopus Shawii is a fine species of the rather extensive genus *Campylopus*, and is distinguished from its nearest British congeners by its great size and characteristic microscopic leaf structure. Hitherto in the British Isles it has been known only from the Outer Hebrides, the Skye group of islands (1), and from West Cork in

Ireland, never having been recorded on the mainland of Scotland. Its occurrence along the north shore of Loch Torridon is thus of considerable interest.

With regard to the second part of the paper—the ecological aspect—all that can be attempted is a presentation of a few outstanding facts concerning the bryophyte communities and the importance of particular species of bryophytes in those assemblages of higher plants which comprise the larger tracts of vegetation. In so brief a visit it was not practicable to attempt any comprehensive analysis of habitat types such as was attempted for the Island of Barra on an earlier occasion (6). It is hoped, however, that the data included here may go to supplement in some degree the rather meagre information which is on record concerning some bryophyte communities in “The British Islands and their Vegetation” (4). At the same time, certain well-marked communities in which Tansley has noted the conspicuous part played by bryophyte species in the composition of the whole, are well seen in the Torridon district. This is particularly true of the ground flora of the coniferous plantations in the Forest of Damph, where certain mosses comprise a very distinct community akin to that described by P. W. Richards (3) (and reported by Tansley) from the Killarney woods in S.W. Ireland.

SYSTEMATIC LIST OF MOSS SPECIES NOTED IN THE TORRIDON DISTRICT (SEPT. 1944).

Sphagnaceae.

Sphagnum plumulosum Roell.

S. compactum DC.

S. papillosum Lindb.

S. cymbifolium Ehrh.

Andreaeaceae.

Andreaea petrophila Ehrh.

A. alpina Smith.

A. Rothii Web. & Mohr.

Polytrichaceae.

Oligotrichum hercynicum Lam.

Polytrichum aloides Hedw.

P. piliferum Schreb.

**P. formosum* Hedw.

P. commune L.

Dicranaceae.

Ditrichum homomallum Hampe.

Swartzia montana Lindb.

Ceratodon purpureus Brid.

Dicranella heteromalla Schp.

D. squarrosa Schp.

Campylopus Schwarzii Schp.

C. flexuosus Brid.

C. pyriformis Brid.

C. fragilis B. & S.

**C. Shawii* Wils.

C. atrovirens De Not.

Dicranum scoparium Hedw.

**D. scoparium* var. *spadiceum*
Boul.

D. majus Turn.

* Not previously reported for V.C. 105.

- D. fuscescens* Turn.
Leucobryum glaucum Schp.
 Grimmiaceae.
Grimmia apocarpa Hedw.
G. maritima Smith.
Racomitrium aciculare Brid.
R. fasciculare Brid.
R. heterostichum Brid.
 **R. heterostichum* var. *gracilescens*
 B. & S.
R. lanuginosum Brid.
Ptychomitrium polyphyllum
 Fuern.
Hedwigia ciliata Ehrh.
 Orthotrichaceae.
Zygodon Mougeotii B. & S.
 **Ulota Bruchii* Hornsch.
U. crispa Brid.
U. crispa var. *intermedia*
 Braithw.
U. phyllantha Brid.
U. Hutchinsiae Hamm.
 Splachnaceae.
Tetraplodon mnioides B. & S.
 Funariaceae.
Funaria Templetoni Sm.
 Bartramiaceae.
Philonotis fontana Brid.
Breutelia arcuata Schp.
 Bryaceae.
Bryum pseudo-triquetrum
 Schwaeg.
 **B. intermedium* Brid.
- B. capillare* L.
Mnium hornum L.
M. punctatum L.
 Fontinalaceae.
Fontinalis antipyretica L.
 * var. *gracilis* Schp.
 Hookeriaceae.
Pterygophyllum lucens Brid.
 Leskeaceae.
Thuidium tamariscinum B. & S.
 Hypnaceae.
 **Brachythecium rivulare* B. & S.
B. plumosum B. & S.
Hyocomium flagellare B. & S.
Eurhynchium myosuroides Schp.
E. myurum Dixon.
E. rusciforme Milde.
Plagiothecium undulatum
 B. & S.
Hypnum revolvens Swartz.
H. cupressiforme L.
H. cupressiforme var. *filiforme*
 Brid.
H. molluscum Hedw.
 **H. eugyrium* Schp.
H. ochraceum Turn.
H. sarmentosum Wahl.
H. cuspidatum L.
H. Schreberi Willd.
Hylocomium splendens B. & S.
H. brevirostre B. & S.
H. loreum B. & S.
H. squarrosum B. & S.
 **H. triquetrum* B. & S.

Total of species and varieties: 77.

The nomenclature adopted for the Sphagna is that of Warnstorf (5). The nomenclature adopted for the other mosses is that of the "Census Catalogue of British Mosses" (2nd edition), 1926.

* Not previously recorded for V.C. 105.

THE ECOLOGICAL SIGNIFICANCE OF CERTAIN SPECIES AND GROUPS OF SPECIES.

(1) *Moorland and mountain slopes—general survey; slopes of Liathach.* Great tracts of the lower slopes of Liathach are covered in early September by the tall fronds of bracken (*Pteridium aquilinum*), but intervening areas carry a vegetation which is in part Callunetum and in part grass moor. In these intervening areas, especially on the grass moor, certain groups of mosses are conspicuous. Thus, in a general survey, the following were noted:

(a) In the general vegetation of the grass moorland:

Breutelia arcuata; *Campylopus atrovirens*—locally very plentiful; *C. Schwarzii*; *Dicranum majus*; *D. scoparium*; *Hylocomium splendens*; *Hypnum cuspidatum*—in patches on wet ground; *H. Schreberi*; *Philonotis fontana*; *Polytrichum commune*; *Sphagnum* spp.; *Thuidium tamariscinum*.

(b) On exposed surfaces of rock:

Andreaea Rothii; *Hedwigia ciliata*; *Ptychomitrium polyphyllum*; *Racomitrium fasciculare*; *R. lanuginosum*; *Ulota Hutchinsiae*.

(c) On and about rocks in running water:

Brachythecium plumosum; *Eurhynchium rusciforme*.

(d) On wet rocky ledges there developed a rich moss flora, which included:

Brachythecium rivulare; *Bryum pseudo-triquetrum*; *Dicranella squarrosa*; *Hypnum molluscum*; *Hypnum ochraceum*; *Mnium punctatum*; *Philonotis fontana*; *Zygodon Mougeotii*.

(e) On peat banks and peat ledges:

Campylopus pyriformis; *Funaria Templetoni*.

(2) *Moorland and mountain slopes—special group of species in and about small burn, slopes of Beinn Damh.* The following occurred here (altitude 1000–1500 ft.):

Fontinalis antipyretica var. *gracilis*—in the burn; *Hylocomium flagellare*; *Pterygophyllum lucens*; *Sphagnum plumulosum*; and in a shallow bog-pool near the source of the burn—*Hypnum revolvens*; *H. sarmentosum*.

(3) *Moorland and mountain slopes—intensive study of the moss flora of boulders, with reference to zonation of species from the bed of the Torridon river up to the adjacent moorland slopes.* With a view to

obtaining some picture of the above-mentioned zonation of moss species the following observations were made:

(a) The following could be classed as riverside boulder species, since they grew close to the water at a level which made them liable to periodic submersion:

Eurhynchium rusciforme; *Fontinalis antipyretica*; *Racomitrium aciculare*; *R. fasciculare*.

(b) The following mosses were taken from a single boulder, 4-5 feet above river water-level at the time of observations:

Hypnum cupressiforme; *Racomitrium aciculare*; *Racomitrium fasciculare*.

(c) The following mosses were taken from boulders bordering riverside path, at edge of moorland and beyond immediate influence of river water:

Andreaea petrophila, loc. f.; *A. Rothii*, loc. f.; *Campylopus atrovirens*, o.; *Hypnum cupressiforme*, f.; *Racomitrium fasciculare*, d.; *R. heterostichum* var. *gracilescens*, f.; *R. lanuginosum*, f.

(4) *Exposed boulders—sample census counts.* (a) With a view to obtaining data on the relative frequency of species in a sample stretch of boulders, a full examination was made of a series of sample boulders, taken at intervals of 10 yards over a 100-yard strip of terrain. The boulders formed an irregular wall, a few feet above sea-level, on the north shore of Loch Torridon. The results are shown in the accompanying table.

Species of Moss.	Boulders Examined.										Totals of Occurrences.
	1	2	3	4	5	6	7	8	9	10	
<i>Dicranum scoparium</i> .	.	.	.	.	.	.	.	×	.	.	1
<i>Eurhynchium myosuroides</i> .	.	.	.	.	.	.	.	.	.	×	1
<i>Eurhynchium Myurum</i> .	×	.	×	×	.	.	.	.	.	.	3
<i>Hypnum cupressiforme</i> .	×	.	.	×	×	.	.	.	.	.	3
<i>Ptychomitrium polyphyllum</i>	.	×	.	.	×	.	×	.	.	×	4
<i>Racomitrium aciculare</i> .	.	.	×	.	.	.	.	.	.	.	1
<i>Racomitrium lanuginosum</i>	.	.	.	.	.	.	.	×	.	.	1
Total species of moss per boulder	2	1	2	2	2	0	1	2	0	2	14

It may be mentioned that the liverwort *Frullania Tamarisci* formed conspicuous patches on boulders 3, 5 and 9.

(b) Full analysis of the moss flora of a single favourably placed sample boulder, on the north shore of Loch Torridon, revealed the following species:

Dicranum scoparium; *Grimmia apocarpa*; *Hedwigia ciliata*; *Ptychomitrium polyphyllum*; *Racomitrium heterostichum*; *Ulota Hutchinsiae*.

(c) Full analysis of a sample boulder on the south shore of the loch yielded the following:

Andreaea petrophila; *Campylopus atrovirens*; *Hypnum cupressiforme*; *Racomitrium fasciculare*; *R. heterostichum*.

(5) *Exposed boulders—altitudinal zonation.* (a) The following species were taken from a boulder almost at sea-level, at the head of Loch Torridon:

Campylopus flexuosus; *Dicranum fuscescens*; *Grimmia maritima*.

(b) Observations were made of the mosses present on and about the base of the rock "cairn" on the summit of Beinn Damh (alt. 2958 ft.) and it was found that the following community—consisting in the main of species widely distributed at lower levels—occurred at this site:

Andreaea petrophila; *Bryum capillare*; *Dicranum scoparium*; *Hypnum cupressiforme*; *Hylocomium loreum*; *Racomitrium fasciculare*.

In addition, the following species were identified from the mountain-top detritus vegetation (alt. c. 2500 ft.) on the upper slopes of Beinn Damh:

Andreaea alpina; *A. Rothii*; *Campylopus Schwarzii*; *Racomitrium heterostichum* var. *gracilescens*; *Racomitrium lanuginosum*.

(6) *Margins of boulders, or border-line between rock surface and adjacent moorland.* In contrast with the exposed surfaces of boulders, where mosses, with certain liverworts and lichens, form the initial stage of a xerosere, the border zone between boulder and adjacent moorland (i.e. between rock and peat surfaces, underlying rock often covered by a thin peaty or humus layer) was found to carry a characteristic intermediate community in which the following species were present:

Campylopus atrovirens; *Polytrichum formosum*; *P. piliferum*; *Racomitrium fasciculare*; *R. lanuginosum*; *Sphagnum compactum*.

Here also the liverwort *Pleurozia purpurea* was locally very

abundant and conspicuous, forming extensive patches of deep crimson-purple at the edge of the moor.

(7) *Bare gravelly soil between roadside and moor.* Situations of this type are well-known to support a characteristic moss community which represents an early stage in the development of the sere on disturbed soil. The following species occurred on a patch of bare gravelly soil by the road at the edge of the moor near Inver Alligin:

Dicranella heteromalla; *Ditrichum homomallum*; *Oligotrichum hercynicum*; *Polytrichum aloides*.

(8) *Coniferous woodland floor—Forest of Damph.* (a) An exceedingly rich moss flora was noted on the boulder-strewn forest floor, beneath the mixed coniferous woodland of the Forest of Damph. In this distinctive bryophytic community the following species grew in luxuriant profusion:

Breutelia arcuata; *Dicranum majus*; *D. scoparium*; *Eurhynchium myosuroides*; *Hylocomium loreum*; *H. splendens*; *Hypnum Schreberi*; *Plagiothecium undulatum*; *Polytrichum commune*; *P. formosum*; *Sphagnum* spp.; *Thuidium tamariscinum*.

(b) A small plantation of pines at the head of Loch Torridon was marked by a forest-floor which consisted of a level peaty-humus layer, unbroken by boulders. Here a bryophytic community flourished, consisting of a dense carpet composed of the two species:

Hylocomium loreum and *Thuidium tamariscinum*.

(9) *Epiphytic mosses—Forest of Damph and other small plantations on the shores of Loch Torridon.* The following notes were made on the epiphytic mosses of particular types of tree:

(a) Epiphytic on birch:

Hypnum cupressiforme var. *filiforme*; *Mnium hornum*; *Ulota Bruchii*; *U. crispa*; *U. phyllantha*.

(b) Epiphytic on hawthorn:

Eurhynchium myosuroides; *Hylocomium brevirostre*; *Thuidium tamariscinum*; *Ulota crispa*; *U. crispa* var. *intermedia*.

(c) Epiphytic on Mountain-ash:

Ulota phyllantha.

(d) Epiphytic on conifers (mainly decaying branches of larch and pine):

Ulota Bruchii; *U. crispa*; *Hypnum cupressiforme* var. *filiforme*.

The data presented above are not intended to be regarded as conclusive in themselves with respect to the definition of "characteristic" species. Thus in no sense must it be concluded from the admittedly limited series of observations here recorded on epiphytes that *Ulota phyllantha* has a marked preference for birch and mountain-ash as opposed to the other species of tree cited; or that the moss *Rhacomitrium aciculare* is rigidly confined to rocks close to running water and at low elevations. That such cases of fairly rigid habitat selection do occur among mosses cannot be denied, but many of them are far from being fully known or fully understood at the present day. The observations here recorded can merely furnish data which, taken in conjunction with a large body of similar facts furnished from other sources, may assist towards a solution of some of these problems of habitat selection.

With regard to the role of mosses in the composition of the general vegetation of the region in question, there can be little doubt that they play a conspicuous part in two main connections: (1) in the initial stages of the sere on exposed rock, peat or loose soil surfaces, and (2) in furnishing a major portion of the general vegetation in certain habitats which are not entirely favourable for the growth of the majority of those flowering plants which might otherwise compete successfully with them; both in the open moorland and in the shade of the coniferous plantations (*e.g.*, in the Forest of Damph) this can be seen. It is well known that those features of the oceanic climate which render Western Europe suitable as a whole for the growth of a rich bryophytic flora are accentuated on the Atlantic coast of Britain, and this has resulted in a notably luxuriant growth of mosses in several distinct types of situation in the Torridon district. Outstanding among these instances is that of the Forest of Damph, where both the boulder-strewn forest floor and the branches of trees exhibit moss communities which cannot readily be paralleled in comparable situations on the east coast. As already suggested, comparison is invited rather with the still richer bryophytic vegetation of the Killarney woods.

In the Torridon district certain mosses—normally recognised as alpine or sub-alpine in their distribution in Britain—may be seen growing at elevations near to sea-level, a phenomenon comparable with the well-known descent of numerous alpine flowering plants to sea-level in parts of north-west Scotland. The outstanding instance of this among the mosses was *Andreaea alpina*, which grew luxuriantly on rocks at low levels on the north shore of Loch Torridon. It is perhaps notable too that the summit "cairn" of

Beinn Damh was characterised by an association of mosses only one of which (*Andreaea petrophila*) could be regarded as an alpine species.

In conclusion, I would thank Mr. J. B. Duncan of Berwick-on-Tweed, who has been good enough to confirm the identification of all critical species, and Mr. W. R. Sherrin of the South London Botanical Institute, who has kindly named the *Sphagna* listed in this paper.

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A LIST OF THE BRYOPHYTES OF BERWICKSHIRE (WATSONIAN
VICE-COUNTY 81). By J. B. DUNCAN.

(Read 13th June 1946.)

The following list of the mosses of Berwickshire is based on "The Moss Flora of the Eastern Borders", by James Hardy (Transactions of the Berwickshire Naturalists' Club, 1868). Hardy tells us that this paper was the result of the work of himself, and several friends—J. and W. B. Boyd and A. Jerdon, with their correspondents, W. Shaw and J. Anderson, during a period of three years. The area included in its scope was Berwickshire, Northumberland (including North Durham) and Roxburghshire. The order of arrangement used was that of "Bryologia Britannica", by W. Wilson, 1855. For this large area Hardy records 267 species. If we deduct some 10 species of *Sphagna* and a few errors in determination which I have been able to rectify, the number of the true mosses represented is 250, a satisfactory result for those days.

Until now no list of the Berwickshire mosses has ever been compiled, nor in the intervening years has any contribution of note been made in this field so far as I know. The extension of the list now published is the result of my own work in the county during the years 1924–1938. The nomenclature used is that of the "Students' Handbook of British Mosses", by Dixon and Jameson, 3rd ed., 1924.

In my list of localities Hardy's come first "(Hardy)"—where no source is given the record is my own. Notes on habitat, comparative rarity, etc., refer to the status of the species in the county of Berwickshire, Watsonian Vice-county 81 only. The number of species included is 274, and of varieties, 59. Needless to say this list cannot be assumed to be anything like exhaustive, but it will afford a useful basis for the bryologist who may undertake to carry on the work. A large moorland tract in the Lammermuirs on the northern edge of the county between Soutra Hill and Longformacus has scarcely been touched by the bryologist and it may be expected to yield some noteworthy additions, especially among the *Sphagna* which have not been worked at all. The rainfall of this county of about 260 square miles is low, averaging about 26 inches. The surface of the area is not greatly diversified, there are no large

sheets of fresh water, few rivers and very little natural woodland. The river banks of Tweed, Whitadder, Blackadder and Eye with its tributary the Ale, combined with a number of "deans" on the lesser streams such as Dunglass, Dowlaw and Pease Deans with the Tower Burn provide, perhaps, the most productive ground for the mosses and especially for the hepatics which are shade- and moisture-loving plants.

There is an almost entire absence of sandy coastline and the high rocky cliffs are very dry and exposed, and barren of mosses. Where the coastal cliffs are of sandstone, with shale and limestone bands, they may be productive of a number of interesting species which are of very local occurrence. On the moorland areas which approach the coast in the Grantshouse-Coldingham area the boggy parts are now very much restricted in extent through drainage. As long ago as 1868 it was remarked that the previous fifty years had seen a great change in the surface of the county through agricultural improvements, plantations, drainage, enclosure of waste land, and artificial works of every kind.

Some remnants of natural woodland survive at Pease Dean, Houndwood, Grantshouse, and at North Wood on the Ale Water, as also in the Duns district.

Probably the richest and most attractive habitat for mosses in the county is the banks of the Whitadder between Abbey St. Bathans and Cockburn Mill, especially in the neighbourhood of Elba and Edins Hall, the site of the famous "Broch" and of an old coppermine. Here the river is rapid and forms some deep pools where it has cut through the Silurian rocks. Below Hoardweel at Cockburn Mill these give place to the sandstone and a different type of vegetation. This region was a favourite haunt of Dr. Johnston, the distinguished founder of the Berwickshire Naturalists' Club in 1831.

In Hepatics our county cannot be expected to be rich on account of its easterly position and dry climate. Except for a short list in "Botany of the Eastern Borders", by Dr. G. Johnston in 1853, in which no localities are given, and Macvicar's "Distribution of Hepaticae in Scotland" (Trans. Bot. Soc. Edin., xxv, 1910), where 52 species and varieties with their localities are noted for v.c. 81, no other sources are available.

Our present list contains 82 species and 10 varieties. The nomenclature used is that of the "Students' Handbook of British Hepatics" (2nd ed., 1926), by S. M. Macvicar.

In conclusion, while these lists contain many additions to the Bryophyte flora of Berwickshire and many notes of new localities

for the rarer species, it must be admitted that a few species which most certainly occur have unaccountably been overlooked. Still, I venture to hope that I may have succeeded in laying the foundation for a more adequate and worthy account of the bryophytes of this interesting Border county whose more remote parts have great charm and are as yet almost unaffected by the intrusion of the holidaymaker and tripper.

Mosses.

Andreaea petrophila Ehrh. Rocks chiefly among the hills, occasionally on walls.

Hoardweel; Drakemire Moor; dykes at Bunkle Edge and Preston (Hardy); Hume Craigs; Black Hill, Earlston; Harelaw Hill, Duns.

var. *acuminata* B. and S. By the Whitadder at Elba; Harelaw Hill, Duns; Black Hill, Earlston.

Tetraphis pellucida Hedw. On rotten tree-stumps, peaty soil in woods, occasionally on sandstone rocks. Fruit not common.

Near the Retreat, Abbey St. Bathans (Hardy); Brockholes Wood; Earlston; Langton Burn (c. fr.).

Catharinea undulata Web. and Mohr. On sandy soil or clay in woods, etc. Common.

var. *minor* W. and M. Drakemire.

Oligotrichum hercynicum Lam. Stony and gravelly soil on the hills, usually barren. Very rare.

Harelaw Hill, Duns.

Polytrichum nanum Neck. Sandy ground, woods and heaths. Rare. Hag Wood, Foulden; earth-capped wall near Grantshouse; Bunkle Wood.

P. aloides Hedw. Sandy or peaty banks. Common.

Brockholes Wood; Hag Wood, Foulden; Lamberton Beach; North Wood, Ale Water; Earlston; Duns; Whitadder at Elba.

P. urnigerum L. Dry and stony places, most frequent in hilly districts.

Roadside, Foulden to Hutton Mill (Hardy); Hag Wood, Foulden; Duns; Longformacus; near Hoardweel.

P. alpinum L. Stony and grassy ground on the higher hills. This is noted for v.c. 81 in the "Census Catalogue of British Mosses" and must certainly occur though I cannot give any locality. J.B.D.

P. piliferum Schreb. Dry heaths, earth-covered walls, etc. Common.

- P. juniperinum* Willd. Sandy heaths and waste places. Common.
- P. gracile* Dicks. Peaty moors. Rare.
Moor near Dowlaw Burn.
- P. formosum* Hedw. Woods and dry banks. Common.
- P. commune* L. Wet moors and peat bogs. Very common.
- Buxbaumia aphylla* L. On peaty soil or rotting tree-stumps. Very rare.
On an earthy wall, Brockholes Wood. J. Anderson (Hardy).
- Archidium alternifolium* Schp. On wet bare soil in woods and by moorland roads. Rare.
Hule Moss; roadside to Halliburton, Greenlaw.
- Pleuridium axillare* Lindb. On damp bare earth by ditches and pools. Rare.
Dean near Raeleughhead (Hardy); Drakemire; pool at Hule Moss; near Brockholes.
- P. subulatum* Rabenh. Sandy heaths and moors. Not uncommon. Coldingham Moor; Penmanshiel Moor and Wood; Brockholes Dean; Oldcambus Dean, and sea banks; Dunglass Dean (Hardy); Foulden; near St. Abb's Head.
- P. alternifolium* Rabenh. Wet fields. Not common.
Near Burnmouth; by Whitadder at Clarabad; Foulden; The Hirsell, Coldstream; North Wood; Gallows Hill, Auchencrow; Coldingham Moor.
- Ditrichum tenuifolium* Lindb. Damp sandy banks. Rare and easily overlooked.
Woods at Duns Castle; Drakemire; banks of Dowlaw Dean.
- D. homomallum* Hampe. Sandy banks and crevices of rocks. Not common.
Bowshiel Dean; Penmanshiel Wood; Drakemire (Hardy); Bunkle Wood (J. Anderson); Duns; Longformacus; Marchmont; by Whitadder near Elba.
- D. flexicaule* Hampe. Calcareous rocks and soil. Frequent.
Sea banks near Siccar Point; moors, Penmanshiel; Dunglass Burn; Fleurs Dean; below Milldean; Ale Water; Lauder (Hardy); Foulden Dean; Burnmouth; Coldingham Moor; Ellem Ford; Cockburn Mill.
- Swartzia montana* Lindb. Recorded for v.c. 81 in "Census Catalogue of British Mosses", but I can give no locality.
- Seligeria recurvata* B. and S. Sandstone rocks. Rare.
Foulden Dean; near Newton Farm, Foulden.
- Brachyodus trichodes* Fuernr. Sandstone rocks. Rare.
Lintlaw Burn; Billie Castle (J. Anderson; Hardy).

Ceratodon purpureus Brid. Sandy and peaty soil, walls, etc. Very common.

Cynodontium Bruntoni B. and S. Siliceous rocks. Rare.

Oldcambus Dean; Netherbyres; near Ayton; Preston Bridge (Hardy); Black Hill, Earlston; Hume Craigs.

[*C. polycarpum* Schp. Hardy recorded this species—certainly an error. The plant should come under *C. Jenneri* Stirt. below. J.B.D.]

C. Jenneri Stirt. Rock crevices and walls in hilly parts. Rare.

Bowshiel Dean on a wall (Hardy); Brockholes (J. Anderson); Chesterhill, Lauder (Herb. Hardy).

Dichodontium pellucidum Schp. Rocks by streams. Common.

var. *compactum* Schp. Wester Burn, Dye Water; by pool at Hule Moss.

D. flavescens Lindb. Rocks in beds of streams. Not common.

Ale Water; Dye Water, Longformacus; Whitadder near Hoardweel.

Dicranella heteromalla Schp. Sandy banks in woods and roadsides, etc. Common.

var. *interrupta* B. and S. Hume Craigs.

var. *sericea* Schp. Sandstone rocks at Foulden and on sea banks at Lamberton.

D. cerviculata Schp. Peaty banks and sides of ditches. Rare.

Penmanshiel; Coldingham Moss; Bunkle Wood; Drakemire; Lauderdale (Hardy).

D. crispa Schp. Wet sandy ground. Very rare.

Sea banks at Lamberton.

D. secunda Lindb. Damp stony ground. Very rare.

Sea banks at Lamberton; by Whitadder above Cockburn Mill.

D. rufescens Schp. Wet clay banks. Not common.

By R. Blackadder, Allanton; fields near Press Castle; by Whitadder near Elba; Lintlaw Burn.

D. varia Schp. Damp clay banks. Common.

D. Schreberi Schp. Damp clay soil. Not common.

Ale Mill; fields by Lintlaw Burn; sea banks at Lamberton; by Whitadder near Edins Hall.

var. *elata* Schp. Roadside near Grantshouse.

D. squarrosa Schp. By moorland streams and bogs. Frequent.

Sisterpath Dean; Penmanshiel Moor; Bunkle Wood (Hardy); Coldingham Moor; Dye Water.

Blindia acuta B. and S. On stones in boggy ground. Rare.

Dowlaw Burn.

Dicranoweisia cirrata Lindb. On trees, fences, rocks, etc. Common.
Campylopus flexuosus Brid. Turfy ground in woods, moors and on sandstone rocks. Frequent.

Drakemire; Penmanshiel Moss; Bunkle Wood (Hardy); Burnmouth; Coldingham and Dowlaw Moors.

C. pyriformis Brid. Peaty moorlands, woods and heaths. Common.

C. fragilis B. and S. Sandstone rocks and heathy ground. Not uncommon.

Sea banks, Lamberton; Cove.

C. brevipilus B. and S. Wet moors. Very rare.

Coldingham Moor.

Dicranum Bergeri Bland. Peat mosses. Very rare.

Dogden Moss near Greenlaw.

D. Bonjeani De Not. Bogs and moors. Frequent.

Lamberton Moor; Coldingham Moor (Hardy); Dowlaw Moor; Dye Water.

var. *rugifolium* Bosw. Bunkle Wood; Dogden Moss.

D. scoparium Hedw. Woods, moors, rocks, and tree trunks. Common.

var. *paludosum* Schp. Water-logged ground in plantation, Coldingham Moor.

var. *orthophyllum* Brid. St. Abb's Head.

var. *spadiceum* Boul. Burnmouth; Dogden Moss.

D. majus Turn. Woods and shady banks. Frequent.

Pease Dean (Hardy); Grantshouse; Dowlaw Burn; coast at Burnmouth, Earnsheugh and Siccar Point.

D. fuscescens Turn. On dry rocks and on tree trunks in damp woods. Not uncommon.

Dowlaw Burn; Green Wood; North Wood, Ale Water; Black Hill, Earlston; Langton Dean, Duns; Longformacus.

var. *falcifolium* Braithw. Dowlaw Burn; by the Whitadder near Hoardweel.

D. montanum Hedw. Base of tree trunks and on rotting stumps. Very rare.

Green Wood, near Grantshouse.

Leucobryum glaucum Schp. Common on all the moors.

Fissidens exilis Hedw. Damp clayey soil in woods. Rare.

Green Wood, Houndswood; Greenfield Plantation, Mordington.

F. viridulus Wahl. Clay banks in shady wooded situations. Not common.

Foulden Dean; R. Eye, Ayton; Ale Water; Dowlaw Burn;

- Pease Dean; Dunglass Dean; Burnmouth; by the Tweed, Lennel.
- var. *Lylei* Wils. Foulden Dean; by R. Eye near Ayton.
- F. pusillus* Wils. Shady sandstone rocks. Not common.
Edrington; dean at Paxton House; sea banks, Lamberton; Dunglass Dean.
- F. incurvus* Starke. Clay banks. Rare.
Burnmouth.
- F. bryoides* Hedw. Clay banks, woods, etc. Frequent.
Edrington; Dowlaw Burn; Earlston; Green Wood.
- F. crassipes* Wils. Rocks in river beds. Rare.
Tweed at Paxton; Whitadder below Hoardweel.
- F. osmundoides* Hedw. Moorland bogs. Rare.
Bog near Cross Law, Coldingham.
- F. adiantoides* Hedw. Wet rocks and boggy ground. Not uncommon.
Burnmouth; Hule Moss; Coldingham Moor; Eyemouth; Grants-house.
- F. decipiens* De Not. Damp rocks by streams. Not common.
North Wood (Ale Water); Whitadder near Elba; Pease Dean; sea banks beyond Eyemouth.
- F. taxifolius* Hedw. Bare soil in woods, hedge banks, etc. Common.
- Grimmia apocarpa* Hedw. Rocks and walls. Common.
var. *alpicola* Hook. and Tayl. Rocks in Whitadder at Foulden and Hoardweel; R. Blackadder at Lintmill and Greenlaw.
- var. *rivularis* W. and M. Stream at Mordington; R. Whitadder at Hutton Bridge, Hoardweel, etc.; Dowlaw Burn; Grange Burn; Eye at Grants-house; Longformacus.
- [*G. conferta* Funk. Preston Bridge (Anderson). Recorded by Hardy, but must be considered very doubtful.]
- G. maritima* Smith. Rocks on the coast, abundant in some parts.
Burnmouth, Eyemouth, etc.
- G. pulvinata* Smith. Walls and rocks. Common.
- G. trichophylla* Grev. Rocks and walls. Not uncommon.
Oldcambus; Lintlaw; Hoardweel (Hardy); Coldingham; Lamberton Moor; Foulden; Mordington; Dowlaw Burn; Grants-house; Elba; Hume Craigs.
- G. Stirtoni* Schp. Dry siliceous rocks. Rare.
Coast at Heathery Carr; near Hoardweel; Gordon.
- G. Hartmani* Schp. Siliceous rocks by rivers. Rare.
R. Whitadder, Elba to Hoardweel; Dye Water at Longformacus.

- G. retracta* Stirton. In similar situation and along with the preceding.
Very rare.
S. bank of Whitadder below Hoardweel.
Along with this was also a form with blunt leaves and short nerve.
- G. Doniana* Sm. Siliceous rocks and walls in hilly parts. Not common.
Walls, Penmanshiel and Bowhills Dean; Drakemire Moor (Hardy); stones on Kaims near Kettleshiel.
- G. commutata* Huebn. Siliceous rocks. Very rare.
Rocks by the Whitadder, Hoardweel.
- Rhacomitrium aciculare* Brid. Rocks in streams in the higher ground. Common.
- R. fasciculare* Brid. Rocks and walls chiefly in the hilly districts. Frequent.
Bowshiel Dean; Penmanshiel (Hardy); Lamberton Moor; Foulden; Dowlaw Burn; Grantshouse; Black Hill, Earlston; Hume Craigs; Hoardweel.
- R. heterostichum* Brid. Rocks and walls. Common.
var. *alopecurum* Huebn. Railway cutting near Grantshouse.
- R. lanuginosum* Brid. Moors and dry stony ground. Common.
- R. canescens* Brid. Stony and barren places in the hills and sandy roadsides. Frequent.
Lammermuirs (Hardy); Coldingham Moor; Grantshouse.
var. *ericoides* B. and S. Coldingham Moor (Hardy); Dye Water; by Whitadder below Hoardweel.
- Ptychomitrium polyphyllum* Fuern. Siliceous rocks and walls in hilly parts. Not uncommon.
Lumsden Dean (Dr. Johnston); Bowshiel Dean; Penmanshiel; near St. Helen's Church; Pease Burn; Netherbyres; Blackhouse; Bunkle and Lintlaw (Hardy); Burnmouth; Dowlaw Burn; railway bank, Eyemouth; Longformacus.
- Hedwigia ciliata* Ehrh. Siliceous rocks and walls in the hilly districts. Not common.
By the Whitadder at Elba and Cockburn Mill; Hume Craigs; Longformacus; Gordon.
- Acaulon muticum* C. M. Bare earth in fields and on wall-tops. Rare.
Oldcambus (Hardy); sea banks near Eyemouth.
- Phascum cuspidatum* Schreb. Fallow fields and waste places. Frequent.
Edrington; Siccar Point.
var. *piliferum* Hook and Tayl. Coast at Siccar Point (Hardy); Eyemouth.

Pottia recta Mitt. Bare ground. Very rare.

At base of sea cliffs, Burnmouth.

P. Heimii Fuernr. Sea banks and salt marshy ground. Not common.

Cove shore; Greenheugh; below Dowlaw; Coldingham sands;

Lamberton Shields (Hardy); Eyemouth.

P. truncatula Lindb. Fallow fields, etc. Common.

P. intermedia Fuernr. Fallow fields, etc. Frequent.

Sea banks, Lamberton.

var. *littoralis* (Mitt.). Coast near Eyemouth.

P. crinita Wils. Rocky banks on the coast. Rare.

Burnmouth; Eyemouth; St. Abb's Head.

P. minutula Fuernr. Bare sandy ground. Rare.

By the sea, Eyemouth, and on the sea banks to the north.

P. lanceolata C. M. Calcareous ground and banks. Rare.

Sea banks at Greenheugh, Oldcambus; Coldingham sands;

Eyemouth; Ale Water (Hardy); Burnmouth; coast at

Lamberton.

Tortula pusilla Mitt. Calcareous banks. Very rare.

Sea banks, Burnmouth.

T. ambigua Ångstr. Calcareous ground. Rare.

Sea banks at Greenheugh (Hardy); Cove; in a railway cutting near Eyemouth.

T. aloides De Not. Calcareous rocks, banks and walls. Not frequent.

Sea banks behind St. Helen's Church; Burnmouth (Hardy);

Lamberton coast.

T. atrovirens Lindb. Gritty banks by the sea. Rare.

Sea banks near Oldcambus; Eyemouth Fort and Gunsgreen

(Hardy); Burnmouth; Lamberton; Cove.

T. muralis Hedw. Rocks, walls and stones. Very common.

var. *rupestris* Schultz. Sandstone cliffs between Eyemouth and St. Abb's.

var. *aestiva* Brid. Paxton; dean at Milne Graden; Ladykirk; Edrington.

T. subulata Hedw. Sandy banks. Frequent.

Burnmouth; Dowlaw Burn; Grantshouse; Fast Castle; Edrington;

Hoardweel; Greenlaw; St. Abb's Head.

T. angustata Wils. Exposed sunny banks. Rare.

By the Tweed below Lennel; Pease Dean.

T. mutica Lindb. Base of trees, rocks and boulders by the larger streams. Not common.

- R. Whitadder at Edrington and Cockburn Mill; Blackadder at Allanton; Tweed at Horndean.
- T. laevipila* Schwaeg. Trunks of trees. Frequent.
Dunglass Dean; Lauder (Hardy); Cumledge Bridge; Ayton; Earlston; Longformacus; Marchmont; Duns.
- T. intermedia* Berk. Calcareous rocks and soil. Frequent.
Burnmouth; St. Abb's; Ale Water; Cockburn Mill.
- T. ruralis* Ehrh. Stony ground, walls and roofs. Not common.
Cottage roof at Cockburnspath old tower (Hardy); Burnmouth; Hume; Byrecleuch on roof.
- T. ruraliformis* Dixon. Sand dunes and all sandy shores. Common.
- T. princeps* De Not. Whinstone rocks. Very rare.
Rocks at Hume Castle.
- T. papillosa* Wils. Tree trunks. Not common.
On plane, elm and ash near Slighhouses; on crab apple, Lintlaw (J. Anderson); Woodhead, Lauder (Hardy); Duns Castle; Cumledge Bridge; Ayton; Ladykirk; Dunglass; Edrington; Longformacus. On intrusive rock, coast at Linkin Shore.
- Barbula lurida* Lindb. Rocks and stonework, generally near water.
Not uncommon.
Whitadder at Hutton Bridge; Cockburn Mill; Blackadder at Kellow; sea banks, Lamberton.
- B. rubella* Lindb. Rocks and walls. Frequent.
Pease Dean; Oldcambus; Dunglass Dean; Dowlaw Dean; Ale Water (Hardy), etc.
- B. tophacea* Mitt. Wet calcareous rocks and banks. Common, especially near the coast.
var. *acutifolia* Schp. Lamberton Beach.
- B. fallax* Hedw. Clay banks, waste places, walls, etc. Very common.
var. *brevifolia* Schultz. Edrington; Lintmill, Greenlaw.
- B. spadicea* Mitt. Rocks and boulders by streams. Not uncommon.
R. Eye at Ayton; Dowlaw Burn; Ale Water; Pease Dean; Langton Burn; Dye Water, Longformacus; R. Whitadder at Elba.
- B. rigidula* Mitt. Walls and rocks. Frequent.
Duns; Ladykirk; Cockburn Mill; Eyemouth; Cove; Longformacus; Hume Castle; Preston; Earnsheugh.
- B. Nicholsoni* Culmann. Rocks and boulders by river banks. Rare.
Tweed at Ladykirk; Whitadder at Edrington and at Hutton Bridge and Ninewells.
- B. cylindrica* Schp. Walls, rocks, banks of streams. Common.

- B. vinealis* Brid. Sandstone walls and rocks. Rare or overlooked.
Burnmouth; Lamberton Shields.
- B. Hornschuchiana* Schultz. Gritty roadsides, old quarries, etc.
Rare.
Foulden; Earlston; near Press Castle.
- B. revoluta* Brid. On mortar of walls. Frequent.
Penmanshiel; near coppermine, Elba (Hardy); Burnmouth;
Eyemouth, etc.
- B. convoluta* Hedw. On waste ground, wall tops, etc. Frequent.
Lamberton Moor (Johnston); Penmanshiel; Bunkle (Hardy);
Grantshouse, etc.
var. *Sardoa* B. and S. Burnmouth.
- B. unguiculata* Hedw. Banks, walls and bare ground. Common.
var. *cuspidata* B. and S. Burnmouth.
- Leptodontium flexifolium* Hampe. Peaty soil. Not common.
Brockholes (J. Anderson).
- Weisia microstoma* C. M. Dry banks. Frequent.
Burnmouth; Eyemouth; Penmanshiel Moor.
- W. tortilis* C. M. Calcareous rocks and banks. Rare.
Siccar Point (Hardy); Burnmouth; St. Abb's Head.
- W. crispata* C. M. Calcareous rocks and banks. Rare.
Burnmouth.
- W. viridula* Hedw. Dry banks. Frequent.
Burnmouth; Ayton Hill; Grantshouse; Earnsheugh; Earlston;
Auchencrow; Greenlaw; Lamberton.
var. *densifolia* B. and S. Rocks by the Whitadder at Elba.
- [*W. mucronata* B. and S. Clay banks. Rare.
Hardy records this from a number of localities, but I think obviously in mistake. I have failed to find it in the area and a specimen of Hardy's which I have examined proved to be *W. tortilis*.]
- W. tenuis* C. M. Damp faces of sandstone rocks. Rare.
Langton Lees Burn; quarry at Preston (Hardy); Foulden Dean;
by Whitadder at Paxton.
- W. rupestris* C. M. Damp rocks. Rare.
Abbey St. Bathans (W. B. Boyd); sea cliffs near Coldingham
Loch; in a small dean near Earnsheugh.
- W. curvirostris* C. M. Wet rocks. Rare.
Near Coldingham (c. fr.) (Hardy); sea cliffs, Lamberton; between
Eyemouth and Coldingham; also at Cove.
- var. *commutata* Dixon. Dripping rocks at Coldingham shore;
Heathery Carr; Lamberton.

W. verticillata Brid. Wet limestone and sandstone rocks. Frequent, often fruiting.

Eyemouth; Coldingham (Hardy); Lamberton shore; Ayton; Foulden Dean; Milne Graden; Cove; Tweed Mill, Lennel.

Trichostomum crispulum Bruch. Calcareous rocks and banks, chiefly near the sea. Rare.

Fleurs Dean, Coldingham; Ale Water; Oldcambus (Hardy); Burnmouth; Earnsheugh; Eyemouth; Cove.

var. *elatum* Schp. Damp shaley rocks, sea cliffs at Lamberton.

var. *littorale* Dixon. Coast at Siccar Point; Redheugh; Coldingham (Hardy); St. Abb's; Dowlaw Burn; Earnsheugh; Ellemford; Cove; Whitadder at Elba and Cockburn Mill.

T. flavovirens Bruch. Sandy ground and banks by the sea. Not common.

Siccar Point (Hardy); Burnmouth; Fast Castle; Cove; St. Abb's Head; Lamberton.

A form with tapering acute leaves also occurs. J.B.D.

T. tortuosum Dixon. Damp rocks. Rare.

Cliffs at Heathery Carr, N. of St. Abb's Head—it must occur elsewhere.

Cinclidotus fontinaloides P. Beauv. Rocks and boulders in streams. Frequent.

Dowlaw Dean; Mill Dean, Coldingham; Ayton; Ale Water (Hardy); Whitadder at Elba, Cockburn Mill, etc.; stream at Heathery Carr.

Encalypta vulgaris Hedw. Dry rocks, walls and banks, especially on calcareous soil. Not common.

Near Eyemouth; Mordington House; Redheugh (Hardy); Burnmouth; Ale Water; Hume Castle; old tower, Cockburnspath; Lintmill, Greenlaw; Edrington; Gavinton.

E. streptocarpa Hedw. Calcareous rocks and mortar of walls. Not uncommon. Very rare in fruit.

Ale Water, below Ale Mill; Eye near Eyemouth; wall near Elba (Hardy); Dowlaw Burn; Grantshouse; Press Castle; Langton, Duns; Edington; Longformacus (c. fr.).

Zygodon Mougeotii B. and S. Damp rocks in the hilly parts. Rare.

By the Whitadder, Edins Hall (Hardy); also near Hoardweel.

Z. viridissimus R. Brown. Tree trunks, occasionally on rocks and walls. Frequent.

Ale Water; Mildean, Coldingham; Pease Dean; Lauder Castle (Hardy); Burnmouth; Ayton; Foulden Dean; Chester Hill,

Burnmouth; Dowlaw Dean; Edrington; Longformacus; Marchmont; Hume Castle; Allanton.

var. *rupestris* Hartm. Siccar Point (Hardy); Chester Hill, Burnmouth; Heathery Carr near St. Abb's Head; Hume Castle.

Z. Stirtoni Schp. Rocks, chiefly near the sea. Frequent.

Burnmouth; Eyemouth; St. Abb's; Ale Water; R. Eye at Ayton; Dowlaw Burn; Earnsheugh; Cove; Lamberton.

Ulota Drummondii Brid. Chiefly on hazel trees in damp hilly parts. Rare.

Penmanshiel Wood; Blackburn-rigg Dean (Hardy); Dowlaw Burn; dean above Langton, Duns; Pease Dean; Green Wood; by the Whitadder near Edins Hall.

U. Bruchii Hornsch. Trees, usually by streams. Frequent.

Pease Dean; Dowlaw Dean; Brockholes Dean; Elmford Farm (Hardy); Foulden Dean; Grantshouse; ravine at Earnsheugh; Cockburn Mill; Allanton; Press Castle; Auchencrow; Langton, Duns; Longformacus.

U. crispa Brid. Trees in damp woods. Frequent.

Hag Wood and Foulden Dean; Ale Water; Allanton; Dowlaw Dean; Press Castle; Earlston; Langton, Duns; Longformacus; near Sisterpath.

var. *intermedia* Braithw. Hag Wood, Foulden; Ale Water; Dowlaw Dean.

U. phyllantha Brid. Trees and rocks near the sea. Not uncommon.

Dowlaw Dean; Siccar Point; near Eyemouth; Brockholes (Hardy); Ayton; Heathery Carr and St. Abb's Head; Foulden; North Wood, Ale Water; Pease Dean; Hume.

Orthotrichum rupestre Schleich. Rocks and walls in the hilly parts. Not common.

Hoardweel (Dr. Johnston); wall, Penmanshiel (Hardy); near St. Abb's Head; Coldingham Loch; Dowlaw Dean; Earnsheugh; by R. Whitadder at Elba.

O. ancmalum Hedw. Siliceous rocks. Very rare: the var. frequent. Rocks by the Whitadder above Cockburn Mill.

var. *saxatile* Hedw. St. Abb's Head; Coldingham Loch; R. Whitadder at Cockburn Mill; Hume Castle.

O. cupulatum Hoffm. Rocks and walls and on boulders on river banks. Frequent.

Oldcambus (Hardy); Mordington; Hutton Bridge; Dowlaw Dean; Heathery Carr; by the Blackadder at Kellow and Greenlaw.

var. *nudum* Braithw. Hutton Bridge; Hoardweel; Cockburn Mill.

O. leiocarpum B. and S. Trees. Rare.

Longformacus.

Hardy says of this, "On trees, common"; but this certainly is not the case. J.B.D.

O. Lyellii Hook and Tayl. Trunks of old trees. Frequent. Rarely fruiting.

Dunglass Dean; Blackhouse; Preston; Lauder (Hardy); Coldingham; Foulden; Dowlaw Dean; Milne Graden; Allanton; Earlston; Hume; Dunglass Dean (c. fr.); Longformacus; Marchmont.

O. affine Schrad. Trunks of trees. Common.

var. *rivale* Wils. Tree roots on banks of the Whitadder at Hoardweel and Ninewells.

O. rivulare Turn. Rocks and tree roots on river banks. Not common.

Bowshiel Dean; Pease Burn; R. Eye at Reston, Ayton and Houndwood; Whitadder at Edrington and Abbey St. Bathans; Longformacus.

O. stramineum Hornsch. Tree trunks. Frequent.

High-houses; near Eyemouth (Hardy); Foulden; Ale Water; Dowlaw Dean; Allanton; Longformacus; Press Castle; Gordon.

O. tenellum Bruch. Tree trunks. Rare.

On elder, Witches Knowe, Lamberton; horse-chestnut at Retreat House, Abbey St. Bathans; West Loch, Coldingham.

O. pulchellum Smith. Trees in damp shady situations. Not uncommon.

Penmanshiel Wood, Bowshiel Dean; Blackburn Rigg Wood (Hardy); Grantshouse; The Hirsell, Coldstream; Cockburn Mill; Greenfield, Mordington; Ale Mill; Allanton; Earlston; Sisterpath; Duns; Whitadder at Elba; Dunglass Dean.

O. diaphanum Schrad. Trees, fences, walls and rocks. Frequent. Burnmouth; Eyemouth, etc.

Splachnum ampullaceum L. On cattle dung in boggy ground. Rare. Penmanshiel Moor; Coldingham Moor (Hardy).

S. sphaericum Linn. fil. On sheep droppings on the higher moors. Not common.

Dogden Moss; moor near the Mutiny Stones, Dye Water.

Tetraplodon mnioides B. and S. On decaying animal matter. Rare.

Penmanshiel Moor; Drakemire (Hardy); Hog's Law, Lauder (Herb. Hardy).

Ephemerum serratum Hampe. Fallow fields. Not common.

Lintlaw (Hardy); Burnmouth; near Green Wood, Houndswood.

Physcomitrium pyriforme Brid. Clay banks and sides of ditches.

Not common.

Edrington.

Funaria fascicularis Schp. Fallow fields. Not common.

Fields near St. Abb's Head.

F. ericetorum Dixon. Sides of moorland ditches. Not common.

Langtonlees Cleugh (Brown); Penmanshiel and Oldcambus Moors;
burn side near Ellemford (Hardy).

F. hygrometrica Sibth. Heaths, banks, woods, etc., especially
where the ground has been burned. Very common.

Amblyodon dealbatus P. Beauv. Boggy ground. Rare.

Ale Water near the Tile Works; Gunsgreen (Hardy).

Aulacomnium palustre Schwaeg. Bogs and wet moors. Very
common.

Bartramia ithyphylla Brid. Rock crevices in hilly districts.
Frequent.

Brockholes; Allanton; Cockburn Law (Hardy); Dowlaw Dean;
Earnsheugh; Ellemford; Hume Crag; Auchencrow, on wall;
Longformacus; Greenlaw.

B. pomiformis Hedw. Rock crevices and sandy banks. Frequent.
Cumledge Mill; Dowlaw Burn; Black Hill, Earlston; Hume
Crag; Longformacus; Greenlaw; Marchmont; Whitadder at
Elba.

var. *crispa* B. and S. By the Whitadder at Hoardweel.

Philonotis fontana Brid. Bogs, springs and river banks. Frequent.
Foulden; Lamberton and Coldingham Moors; Earlston, etc.

P. calcarea Schp. Calcareous bogs and springs. Not common.

Ewehole (Anderson); Lamberton Moor; sea banks near Lam-
berton; Tweed Mill; Coldingham Loch (Herb. Hardy).

P. capillaris Schp. Clefts of rocks by springs, damp woodland
pathways, etc. Rare.

Hag Wood, Foulden; The Hirsell, Coldstream; North Wood, Ale
Water; Longformacus; Hoardweel.

Breutelia arcuata Schp. On wet moors. Rare and local.

Coldingham Moor; Lamberton Moor (Johnston); Drakemire
(Hardy).

Leptobryum pyriforme Wils. Sandstone rocks; often appears in
hothouses. Rare.

This must occur though I have no record for it in a feral state.
J.B.D.

- Webera cruda* Schwaeg. Clefts of rocks in hilly parts. Frequent.
 Oldcambus; Ale Water; Whitadder at Ellem Ford and near
 Hoardweel (Hardy); Dowlaw Burn; Earlston; Hume Crags;
 Blackadder near Lintmill.
- W. nutans* Hedw. Peaty and sandy soil, woods and moors. Very
 abundant.
- W. annotina* Schwaeg. Sandy places. Rare.
 Longformacus.
 var. *erecta* Correns. Hag Wood, Foulden; Bunkle Wood; Pen-
 manshiel Moor; Hule Moss; Gordon Moss.
 var. *bulbifera* Correns. Green Wood, Houndswood; Penmanshiel
 Moor; Bunkle Wood; Duns; Marchmont.
- W. prolifera* Bryhn. Sandy ground and rocks. Rare.
 Railway cutting, Grantshouse; by Whitadder near Elba.
- W. carnea* Schp. Clay banks by streams. Not uncommon.
 Pease Dean; Greenheugh; Oldcambus; Penmanshiel; Dunglass
 Dean; coast near Coldingham; old quarry, Lintlaw; Nether-
 byres (Hardy); Foulden Dean; near Edrington.
- W. albicans* Schp. Clay banks, springs. Frequent.
 Pease Dean; near Cockburnspath tower; railway bank near
 Reston (Hardy); Lamberton beach; Dunglass Dean.
- Bryum filiforme* Dicks. Wet rocks by hill streams. Rare.
 Primrose Hill (J. Anderson); Whitadder near Elba.
- [*B. pendulum* Schp. Walls and dry heaths.
 We have overlooked this in Berwickshire and I can give no locality.
 though it must certainly occur. J.B.D.]
- B. pallens* Sw. By streams and wet places. Common.
 Preston Bridge (Hardy); Burnmouth; Lamberton beach;
 Edrington; Duns; Greenlaw.
- [*B. Duvalii* Voit. Hardy recorded this from Drakemire but the
 specimen proves to be a form of *B. pallens*. J.B.D.]
- B. pseudo-triquetrum* Schwaeg. Bogs and wet places. Frequent.
 especially in the hills.
- B. bimum* Schreb. Bogs and pools. Rare.
 Small pool on Lamberton Moor.
- B. intermedium* Brid. Damp, sandy ground, walls, etc.
 Frequent.
 On a wall, Oldcambus; Ale Water; above Billy Mill (Hardy).
- B. caespiticium* L. Rocks and walls. Common.
 Dowlaw Burn.
- B. capillare* L. Rocks, walls and tree trunks. Abundant.
 var. *flaccidum* B. and S. Wooded stream, Press Castle.

var. *elegans* Braithw. Dry rocks, Heathery Carr beyond St. Abb's Head.

B. erythrocarpum Schwaeg. Sandy heaths.

The "Census Catalogue of British Mosses" records this for Berwickshire. It is certain to occur but I cannot give any locality. A very easily overlooked plant unless in good fruiting condition.

B. atropurpureum W. and M. Roadsides, wall tops, waste places. Abundant.

var. *gracilentum* Tayl. Horndean; by pond, moor near Mordington.

B. alpinum Huds. Wet rocks. Rare.

On gravelly road, Penmanshiel Moor.

B. argenteum L. Waste ground, roofs, etc. Abundant.

var. *lanatum* B. and S. In very dry, warm spots. Less frequent.

B. roseum Schreb. Shady banks in woods. Rare.

Oldcambus (Hardy); Blackhouse Dean (Anderson); Dowlaw Dean.

[*Mnium affine* Bland. Not recorded for Berwickshire, and I have unaccountably overlooked it. It must certainly occur. J.B.D.]

M. cuspidatum Hedw. Damp ground in woods. Rare.

By a wall, Penmanshiel Farm (Hardy).

M. rostratum Schrad. Rocks and banks by streams. Frequent.

Pease Dean; Dunglass Dean; Fleurs Dean; Ale Water (Hardy);

R. Eye at Ayton; Whitadder at Hoardweel; Paxton House.

M. undulatum L. Woods. Abundant.

M. hornum L. Woods, rocks, roots of trees. Very abundant.

M. serratum Schrad. Rocks, usually by streams. Not common.

Langtonlees Cleugh; near Cockburn Law (Hardy); Whitadder at Ninewells.

M. stellare Reich. Rocks by streams and in shady places. Not common.

Oldcambus (Hardy); Brockholes Dean (Anderson); Dowlaw Dean; Pease Dean; R. Leader, Earlston; Ninewells.

M. punctatum L. Rocks and stones by streams. Common.

M. subglobosum B. and S. Bogs. Rare.

Drakemire (J. Anderson).

Fontinalis antipyretica L. Rivers, ponds and pools. Common.

Cryphaea heteromalla Mohr. Tree trunks. Rare.

Ayton Woods; Sligh-houses (Hardy); Cockburn Mill (J. Anderson); Witches Knowe, Mordington.

Neckera crispa Hedw. Dry rocks. Rare.

Earnsheugh (Hardy); Dowlaw Dean; by R. Leader, Cowdenknowes.

var. *falcata* Boulay. Sea cliffs near Earnsheugh.

N. complanata Huebn. Trunks of trees, banks and rocks. Common.

Homalia trichomanoides B. and S. Roots of trees, banks and rocks. Frequent.

Brockholes; near Allanton (Hardy); Foulden Dean; Ayton; Edrington; Ale Water; Dowlaw Dean; Pease Dean; Green Wood; Earlston; Auchencrow; Langton Burn.

Pterygophyllum lucens Brid. Wet banks by streams and among rocks. Widely distributed.

Boggy places on Dirrington; Langtonlees Cleugh; Dunglass Dean; Sisterpath Dean; Penmanshiel Moor (Hardy); sea banks at Lamberton; Dowlaw Dean.

Leucodon sciurioides Schwaeg. Trunks of trees. Rare.

Ayton Woods; near Lauder (Hardy); Cumledge Bridge; near Marchmont Church; Gordon Tower.

Pterogonium gracile Swartz. Rocks and tree trunks. Rare.

Oldcambus; near Ayton (Hardy); St. Abb's Head, on dry rocks overlooking the loch.

Antitrichia curtipendula Brid. Trees, walls and rocks. Rare.

Penmanshiel; Dunglass Wood; on a wall, Lauder to Earlston (Hardy); Foulden Dean.

Porotrichum alopecurum Mitt. Shady woods, walls and rocks by waterfalls. Common.

Leskea polycarpa Ehrh. Tree roots and rocks on river banks. Not common.

Tweed at Horndean; Whitadder near Cockburn Mill.

Anomodon viticulosus Hook and Tayl. Dry, shady wooded rocks. Not common.

Banks of Eye, Ayton; Ale Water; Pease Dean (c. fr.) (Hardy); R. Leader near Earlston; Stitchell Linn.

Heterocladium heteropterum B. and S. Wet rocks by streams—chiefly in the hills. Not common.

Brockholes Wood; Harelaw Wood, Duns.

var. *fallax* Milde. Hoardweel (J. Anderson); Brockholes Wood; Pease Dean; Dowlaw Burn; by the Leader, Earlston.

Thuidium tamariscinum B. and S. Shady woods. Very common.

Climacium dendroides W. and M. Marshy ground. Frequent.

Penmanshiel Moor; Dye Water; Whitadder at Elba, etc.

Pylaisia polyantha B. and S. Trees. Rare.

Ayton Woods; Ale Water (Hardy).

Camptothecium sericeum Kindb. Trunks of trees, rocks and stone walls. Very common.

C. lutescens B. and S. Sand dunes and calcareous banks. Rare.

Near Cockburn Mill; shore at Cove.

C. nitens Schp. Upland bogs. Rare.

Drakemire bog (Anderson); Penmanshiel; near Dowlaw Moss; Elmford and Barnside Marsh, Lammermoors (Hardy); Fangrist Burn, Greenlaw (Duncan).

Brachythecium glareosum B. and S. Calcareous banks. Not common.

Whitadder near Paxton; sea banks, Lamberton; near Whitehall; Cockburn Mill; Pease Dean; Earlston; Langton Burn; Ninewells.

B. albicans B. and S. Sandy soil. Frequent.

St. Abb's; Mordington, etc.

B. salebrosum B. and S.

var. *palustre* Schp. Near Lumsdaine, Coldingham; wet field near St. Abb's Head.

B. rutabulum B. and S. Earth, rocks, walls, trees. Very frequent.

B. rivulare B. and S. Rocks and stones by streams, often submerged. Frequent.

Drakemire; by R. Whitadder (Hardy); R. Eye, Ayton; etc.

var. *chrysophyllum* Bagnall. Pease Dean.

B. velutinum B. and S. Rocks and banks. Not uncommon.

Dowlaw Dean; Green Wood; Mordington; Sisterpath; Brockholes Wood; Pease Dean; Ninewells.

B. populeum B. and S. Walls and stones in shady places. Frequent.

Ayton; Dowlaw Dean; North Wood, Ale Water; Earlston; Longformacus; Duns; Sisterpath; Pease Dean; West Loch, Coldingham.

B. plumosum B. and S. Rocks in and near streams. Frequent.

Coldingham; Edrington; Ayton; Dowlaw Dean; Dunglass Dean; Longformacus.

B. caespitosum Dixon. Rocks and stones by river banks. Rare.

Banks of Tweed near Tweed Mill below Coldstream.

B. purum Dixon. Grassy banks, woods and moors. Very common.

Eurhynchium piliferum B. and S. Woods and banks. Frequent.

Earlston; Auchencrow; Longformacus; Pease Dean; Duns, etc.

E. crassinervium B. and S. Rocks and stones in shady ground. Not uncommon.

- R. Eye at Ayton; Ale Water; Pease Dean; stream near Earnsheugh and Coldingham shore; Whitadder at Hoardweel and Ninewells.
- var. *turgescens* Mol. Dowlaw Burn; stream at Earnsheugh.
- E. speciosum* Schp. Stones near water. Very rare.
Dowlaw Burn where it falls over cliffs to the sea.
(NOTE.—The plant was fruiting and quite definitely distinguishable from any form of *E. Swartzii*. J.B.D.)
- E. praelongum* Hobk. Banks, hedgerows, woods. Very abundant.
var. *Stokesii* Brid. Allanton; Longformacus; Whitadder near Hoardweel.
- E. Swartzii* Hobk. Wet fields and rocks near streams. Frequent.
Foulden Dean; Edrington; Ale Water; Ladykirk; Ayton; Coldstream; Duns.
var. *rigidum* Boul. Dean at Paxton; Eye near Ayton; Pease Dean; near the Whitadder at Whitehall; Allanton and Ninewells.
- E. abbreviatum* Schp. Sandstone rocks and on marly soil. Rare.
Ale Water; Pease Dean; Langton Burn; by R. Tweed below Lennel.
- E. pumilum* Schp. Rocks and stony ground in shady situations. Not uncommon.
Foulden Dean; Clarabad Mill; Ale Water; Dowlaw Dean; Milne Graden; near Earnsheugh; Paxton; Earlston; Pease Dean; Cove; Dunglass Dean; Ninewells.
- E. Teesdalei* Schp. Wet rocks in the beds of small wooded streams. Rare.
Near Coldingham shore; Foulden Dean; Dowlaw Dean; R. Eye near Ayton; near Earnsheugh; Pease Dean.
- E. tenellum* Milde. Calcareous rocks. Rare.
Sea banks near Dowlaw; Ale Water (Hardy); by the Whitadder near Edrington.
- E. myosuroides* Schp. Rocks and tree trunks, especially in hill districts. Common.
Hag Wood, Foulden, etc., etc.
- E. myurum* Dickson. Rocks and tree trunks. Common.
Ayton; rocks near Eyemouth, etc.
- E. striatum* B. and S. On rocks, ground in woods and hedgebanks. Very common.
- E. rusciforme* Milde. Rocks and stones in and near streams. Very common.

- var. *atlanticum* Brid. Small stream on sea cliffs near Coldingham Loch.
- E. murale* Milde. Rocks and walls in shady situations. Frequent. Oldcambus (Hardy); Foulden; Cockburn Mill; Langton Burn.
- var. *julaceum* B. and S. Woods by the Whitadder near Paxton.
- E. confertum* Milde. Walls, stones and tree stumps in shady places. Common.
- Plagiothecium depressum* Dixon. Foot of trees and rocks in shady calcareous ground. Not common.
- R. Eye near Ayton; Ale Water (c. fr.); Dowlaw Dean; Pease Dean; in a small dean near Earnsheugh and by a stream near Coldingham.
- P. elegans* Sull. Siliceous rocks and peaty soil in woods. Frequent. Brockholes Wood (Hardy); Ale Water; Dowlaw Dean; dean at Paxton House; Hag Wood, Foulden; Earlston; Longformacus; Abbey St. Bathans.
- P. pulchellum* B. and S. Among mosses in rock crevices in the hills. Rare.
- Near Edins Hall, Cockburn Law; Buskin Burn, Coldingham Moor; rock fissures near the sea at Siccar Point (Hardy).
- P. denticulatum* B. and S. On soil, roots of trees, rocks, chiefly in woods. Common.
- P. sylvaticum* B. and S. Rocks and banks in woods and deans. Not uncommon.
- Ale Water; Lamberton Beach; Dowlaw Dean; Grange Burn; Pease Dean; Brockholes Wood; Cockburn Mill.
- P. undulatum* B. and S. Upland woods and moors. Frequent.
- P. latebricola* B. and S. On decaying wood. Very rare.
- Brockholes Wood (J. Anderson, 1870; J. B. Duncan, 1926).
- Amblystegium compactum* Aust. On damp calcareous rock ledges. Rare.
- Lamberton Beach; by Whitadder near Paxton; Blackadder near Allanton; Dunglass Dean.
- A. serpens* B. and S. On the ground, stones, decaying wood, etc. Very common.
- A. Juratzkanum* Schp. Tree roots near water, and on damp sandstone rock. Rare.
- Base of willow tree, coast at Lamberton; on sandstone rocks near Cove.
- A. irriguum* B. and S. Rocks and stones in streams. Not common.
- Dowlaw Dean; R. Eye near Ayton; Whitadder at Elba; Ale at Press Castle; Blackadder above Kelloe; Dye Water at

Byrecleuch; Pease Dean; Langton Burn; Westerside. Coldingham.

A. fluvatile B. and S. Rocks and stones in the beds of streams. Not common.

R. Eye, Ayton; Stream near Brockholes; Whitadder at Elba, Cockburn Mill and Cumledge Mill.

A. filicinum De Not. Damp ground, stones and rocks near streams, bogs, etc. Common.

var. *trichodes* Brid. Cliffs at Lamberton; cave between Eyemouth and Coldingham; Langton-Lees Cleuch; Dunglass Dean.

Hypnum riparium L. Roots of trees, stones, etc., by water. Not uncommon in the low ground.

Pond near Ayton.

H. elodes Spruce. Marshy ground. Rare.

Penmanshiel Moor (Hardy); Lamberton Moor.

H. polygamum Schp. Marshy ground usually near the sea. Not common.

Near Eyemouth; Lintlaw Burn; near Lauder (Hardy).

H. stellatum Schreb. Bogs and wet ground. Frequent.

Lamberton Moor; Burnmouth; Ayton Hill; Cross Law, etc.

var. *protensum* Roehl. Damp calcareous rocks. Eyemouth; Burnmouth; Cove.

H. chrysophyllum Brid. Calcareous ground and rocks. Rare.

Sea banks, Lamberton.

H. aduncum Hedw. non L. Marshes and pools. Not common.

Penmanshiel Moor.

H. fluitans L. Peat bogs and pools. Not uncommon.

Lammermoors; Coldingham Moor (Hardy); Dowlaw Moor.

H. exannulatum Güm. Upland bogs. Not uncommon.

Moor near Lumsdaine; Longformacus; Hule Moss.

var. *falcifolium* Ren. Moor near Lumsdaine.

H. uncinatum Hedw. Rocks and walls in upland parts. Not uncommon.

Near Greenlaw; Penmanshiel; Bowshiel Dean (Hardy); Drake-mire; Duns; Longformacus; Marchmont; Gordon.

H. revolvens Swartz. Bogs. Frequent.

Moors, Lamberton; Penmanshiel; Coldingham and Drakemire (Hardy); Ayton Hill; Dogden Moss.

H. commutatum Hedw. Calcareous bogs and dripping rocks. Common.

- H. falcatum* Brid. Bogs. Not uncommon.
Sea banks, Hilton Bay; Lamberton Moor; Coldingham Moor;
coast near Linkin Burn; Dowlaw Burn.
- H. cupressiforme* L. Trees, walls, rocks, etc. Very common.
var. *resupinatum* Schp. Frequent.
var. *filiforme* Brid. Trees. Frequent. Dowlaw Dean; Grants-
house; Ale Water; Press Castle; Longformacus.
var. *minus* Wils. Trees. Rare. Langtonlees Cleuch.
var. *ericetorum* B. and S. Moors and heaths. Common.
var. *tectorum* Brid. Rocks, walls, roofs and sandhills by the sea.
Eyemouth; St. Abb's; Coldingham Loch; Burnmouth;
Auchencrow.
var. *elatum* B. and S. Rare. Dowlaw Dean; near Earnsheugh.
- H. imponens* Hedw. Damp heaths. Rare.
Drakemire; Dogden Moss.
- H. Patientiae* Lindb. Clayey soil in woods and roadside banks.
Not common.
Eyemouth (Hardy); Brockholes; Berryhill (Anderson); Hag
Wood, Foulden; Grantshouse; Ale Mill; Duns; Press Castle;
Whitadder near Hoardweel.
- H. molluscum* Hedw. Calcareous soil and rocks by streams.
Common.
St. Abb's; Dowlaw Burn, etc.
var. *condensatum* Schp. Near Lumsdaine, Coldingham.
- H. crista-castrensis* L. Plantations. Rare.
Blackhouse Dean; Dogbush plantations above Marygold (And-
erson-Hardy); Bunkle Wood.
- H. palustre* Huds. Rocks in and by streams. Frequent.
Lamberton Moor; Ale Water; Foulden Dean; Coldingham
Loch; Dowlaw Dean; Earnsheugh; Allanton; Longformacus;
Greenlaw.
- H. eugyrium* Schp. Rocks in hill streams. Rare.
R. Whitadder, below Edins Hall.
- H. ochraceum* Turn. Rocks in hill streams. Not common.
Dye Water, Longformacus; Whitadder near Elba.
- H. scorpioides* L. Moorland bogs. Not common.
Lamberton Moor; Coldingham Moor (Dr. Johnston); Penman-
shiel Moor; Drakemire (Hardy); Cross Law, Coldingham;
Dogden Moss.
- H. stramineum* Dicks. Hill bogs. Not common.
Chooselea, Langton—in fine fruit (Rev. T. Brown); Penmanshiel
Moss; Drakemire (Hardy).

- H. cordifolium* Hedw. Bogs and pools. Not common.
Langton Woods (Rev. T. Brown); Birgham Moor (Dr. Johnston);
Penmanshiel Moor; Drakemire; near Chirnside Mill (Hardy);
Lamberton Moor; Oldcambus; Coldingham Moor; Gordon
Moss.
- H. giganteum* Schp. Moorland bogs and ditches. Not common.
Penmanshiel Moor; Coldingham Moor and near Cross Law;
Dogden Moss; Lamberton Moor (c. fr.).
- H. cuspidatum* L. Wet ground. Very common.
- H. Schreberi* Willd. Dry woods and heathlands. Very common.
- Hylocomium splendens* B. and S. Heaths and woods. Common.
var. *gracilius* Boul. In very exposed situations. Coast at St.
Abb's Head and Lamberton.
- H. loreum* B. and S. Woods. Frequent.
- H. squarrosum* B. and S. Grassy banks. Abundant.
- H. triquetrum* B. and S. Woods, hedge banks, sandhills. Very
common.

Hepatics.

- Riccia glauca* L. Gavington (Dr. Johnston).
- Reboulia hemisphaerica* (L.) Raddi. Heathery Carr, Earnsheugh;
Dowlaw Burn; R. Whitadder near Hoardweel.
- Conocephalum conicum* (L.) Dum. Frequent on damp rocks.
- Lunularia cruciata* (L.) Dum. Longformacus; Cockburnspath
(Macvicar); St. Abb's; R. Eye, Ayton; Ale Water; Cockburn
Mill.
- Marchantia polymorpha* L. Whitadder near Hoardweel.
- Aneura pinguis* (L.) Dum. Bogs and watery places. Frequent.
- A. incurvata* (Lindb.) Steph. Pease Dean (Macvicar).
- A. multifida* (L.) Dum. Cockburnspath (Macvicar).
- A. sinuata* var. *major* Lindb. Near Earnsheugh; Burnmouth.
- Metzgeria furcata* (L.) Dum. Pease Dean; Longformacus (Mac-
vicar); Burnmouth; Ayton; Mordington; Dowlaw Dean.
var. *fruticulosa* (Dicks.) Lindb. Mordington; Allanton; Cowden-
knowes, Earlston; Sisterpath; Dunglass Dean.
- M. conjugata* Lindb. Cockburnspath (Macvicar); rocks by R.
Leader, Earlston.
- M. pubescens* (Schränk) Raddi. Dowlaw Dean; North Wood, Ale
Water; by R. Leader near Earlston.
- Pellia epiphylla* (L.) Corda. Common.
- P. Fabbriana* Raddi (*J. calycina* Tayl.). Common.
var. *lorea* Nees. Foulden Dean.

- Blasia pusilla* Linn. Cockburnspath (Macvicar); near Press Castle; Longformacus; Wester Burn, Dye Water.
- Fossombronia pusilla* (L.) Dum. Pease Dean (Macvicar); Burnmouth; Preston Haugh; North Wood, Ale Water; Lintlaw Burn.
- F. Wondraczeki* (Corda) Dum. North Wood, Ale Water; field near Press Castle.
- Marsupella emarginata* (Ehrh.) Dum. Tullishill (Macvicar); near Earnsheugh; St. Abb's Head; Bunkle Edge; Penmanshiel Moor; Elba; Hume Crag; Dye Water.
- Alicularia scalaris* (Schrad.) Corda. Common.
- Aplozia crenulata* (Sm.) Dum. Carfrae; Cockburnspath (Macvicar); Foulden; Lamberton Beach; Penmanshiel Moor; Press Castle; Duns; Langton; Longformacus; Hoardweel.
- var. *gracillima* (Sm.) Heeg. Hag Wood, Foulden; Green Wood; Bunkle Wood; Duns.
- A. riparia* (Tayl.) Dum. Cockburnspath (Macvicar); Dowlaw Dean; Earnsheugh; by Whitadder at Elba.
- A. pumila* (With.) Dum. Cockburnspath (Macvicar); Paxton Dean.
- Gymnocolea inflata* (Huds.) Dum. Seenes Law; Tallishill (Macvicar); Coldingham Moor; Black Hill, Earlston.
- Lophozia turbinata* (Raddi) Steph. Cockburnspath (Macvicar); Ale Water; Pease Dean; Cove; Allanton; Eyemouth; Siccar Point; Dowlaw, by the sea.
- L. badensis* (Gottsche) Schiffn. Coldingham; Eyemouth; Clarabad Mill.
- var. *obtusiloba* (Bern.) Schiffn. By a small stream, Coldingham shore.
- L. bantriensis* (Hook.) Steph. Near Dowlaw Burn.
- L. ventricosa* (Dicks.) Dum. Common.
- L. bicrenata* (Schmid.) Dum. Cockburnspath (Macvicar); Bunkle Wood.
- L. excisa* (Dicks.) Dum. Kelhope Glen (Macvicar); woods at Duns.
- L. incisa* (Schrad.) Dum. Gordon Moss.
- L. quinquedentata* (Huds.) Cogn. Threeburnfoot; Cockburnspath; Longformacus (Macvicar); Dowlaw Dean; near Earnsheugh; Edins Hall.
- L. Hatcheri* (Evans) Steph. Hume Crag; Longformacus; Whitadder below Hoardweel.
- L. Floerkii* (Web. et Mohr.) Schiffn. Longformacus; near Cockburnspath; near Seenes Law (Macvicar); Dowlaw Dean;

- Bunkle Edge; Coldingham and Penmanshiel Moors; Black-Hill, Earlston; Hume Craigs; Dogden Moss; woods, Duns.
- L. attenuata* (Mart.) Dum. Cockburnspath (Macvicar); Lamberton Beach; Longformacus; Whitadder near Hoardweel.
- L. barbata* (Schmid.) Dum. Noted for v.c. 81 in "Census Catalogue of British Hepatics" (1930). Though it is likely to occur I cannot give any locality. Dr. Johnston mentions it in his "Flora of the Eastern Borders" but gives no station.
- Sphenobolus exsectiformis* (Breidl.) Steph. Cockburnspath (Macvicar); Lamberton.
- Plagiochila asplenioides* (L.) Dum. Frequent on shady rocks.
- var. *minor* Lindenb. Ale Water; Dowlaw Dean; Hume Craigs.
- var. *humilis* Lindenb. Grantshouse; near Earnsheugh; Chester Hill, Burnmouth.
- var. *major* Nees. Frequent in damp woods.
- Leptoscyphus anomalus* (Hook.) Mitt. Seenes Law (Macvicar); Coldingham Moor.
- Lophocolea bidentata* (L.) Dum. Pease Dean (Macvicar); Burnmouth; near Greenlaw.
- L. cuspidata* Limpr. Common.
- L. heterophylla* (Schrad.) Dum. Cockburnspath; Longformacus (Macvicar); Pease Dean; Dowlaw Dean; North Wood, Ale Water.
- L. fragrans* Moris et de Not. (*L. spicata* Tayl.). Pease Dean (Macvicar); ditto, 1930, J.B.D.
- Chiloscyphus polyanthus* (L.) Corda. Cockburnspath (Macvicar); near St. Abb's Head; Drakemire; Penmanshiel Moor; Grantshouse; Dye Water; Langton Burn.
- Cephalozia bicuspidata* (L.) Dum. Common.
- var. *Lammersiana* (Hüb.) Breidl. Cockburnspath (Macvicar).
- C. connivens* (Dicks.) Lindb. Near Seenes Law (Macvicar); Penmanshiel Moss.
- C. media* Lindb. North Wood, Ale Water; Press Castle; Longformacus; Duns; Dogden Moss.
- C. macrostachya* Kaal. Moor near Press Castle; Dogden Moss.
- C. leucantha* Spruce. On rotting log, Brockholes Wood.
- Nowellia curvifolia* (Dicks.) Mitt. Brockholes Wood; Foulden Dean; Mordington; North Wood, Ale Water; Whitadder near Edrington; Longformacus; Dunglass Dean; Duns Woods; near Abbey St. Bathans.
- Cephaloziella Starkii* (Funck) Schiffn. Frequent.

- Odontoschisma Sphagni* (Dicks.) Dum. Near Seenes Law (Macvicar); Drone Moss; Dogden Moss.
- O. denudatum* (Nees) Dum. Near Seenes Law (Macvicar).
- Calypogeia Trichomanis* (L.) Corda. Near Seenes Law (Macvicar); Coldstream; Penmanshiel Moor; Brockholes Wood; Drone Moss; Duns; Langton.
- C. fissa* (L.) Raddi. Pease Dean (Macvicar); Green Wood; Dunglass Dean; Langton; coast at Lamberton.
- C. arguta* Nees et Mont. Near Press Castle.
- Bazzania trilobata* (L.) Gray. Noted for v.c. 81 in the "Census Catalogue of British Hepatics". Likely to occur but no station can be given.
- Lepidozia reptans* (L.) Dum. Frequent in woods.
- L. setacea* (Web.) Mitt. Dogden Moss; Penmanshiel Moss.
var. *sertularioides* (Hüb.) Cooke. Near Seenes Law (Macvicar).
- Blepharostoma trichophyllum* (L.) Dum. By the Whitadder below Hoardweel.
- Ptilidium ciliare* (L.) Hampe. Near Seenes Law (Macvicar); Hume Craigs; Dogden Moss, etc.
- P. pulcherrimum* (Web.) Hampe. Green Wood; Greenfield plantation, Mordington; woods at Duns.
- [*Trichocolea tomentella* (Ehrh.) Dum. Appears for v.c. 81 in "Census Catalogue of British Hepatics", and mentioned in "Flora of Eastern Borders" (Dr. Johnston), but no locality given.]
- Diplophyllum albicans* (L.) Dum. Very common.
- Scapania compacta* (Roth) Dum. Hume Craigs; Burnmouth; Grantshouse; Lamberton Beach; near Lumsdean; by Whitadder at Elba.
- S. subalpina* (Nees) Dum. By Whitadder at Elba; Dye Water.
- S. gracilis* (Lindb.) Kaal. Sea banks at Lamberton.
- S. nemorosa* (L.) Dum. Penmanshiel Moss; Drakemire; Longformacus.
- S. dentata* Dum. Cockburnspath (Macvicar); Longformacus; Duns; Whitadder near Edins Hall.
- S. undulata* (L.) Dum. Near Seenes Law (Macvicar); Coldingham Moor.
- S. irrigua* (Nees) Dum. Near Seenes Law (Macvicar); Foulden; Drakemire; Bunkle Wood; Hule Moss.
- S. curta* (Mart.) Dum. Cockburnspath; Longformacus (Macvicar); Foulden; sea banks near Lamberton Beach; by R. Leader, Earlston; Drakemire strips.
- S. umbrosa* (Schrad.) Dum. Dunglass Dean.

- Radula complanata* (L.) Dum. Frequent on tree trunks.
- Madotheca Thuja* (Dicks.) Dum. Dry rocks in a small dean near Earnsheugh.
- M. platyphylla* (L.) Dum. R. Eye near Ayton; Chester Hill; Ale Water; Dowlaw Dean; Cockburn Mill; Elba; Allanton; Earlston; Stitchell Linn; Pease Dean; Langton Dean.
- M. Cordeana* (Hüb.) Dum. Pease Dean (Macvicar); Dowlaw Dean; R. Eye below Ayton; by R. Leader, Earlston; Longformacus; by R. Whitadder near Hoardweel.
- Cololejeunea Rossettiana* (Massal.) Schiffn. Pease Dean (Macvicar).
- Lejeunea cavifolia* (Ehrh.) Lindb. Dowlaw Dean; Pease Dean; R. Eye near Ayton; Elba; Grange Burn; Burnmouth; Foulden Dean; Monynut Burn; Whitadder near Edins Hall.
var. *heterophylla* Carr. Dowlaw Dean.
- L. planiuscula* (Lindb.) emend Buch. Dowlaw Dean.
- Frullania Tamarisci* (L.) Dum. Burnmouth; Dowlaw Dean; Hume Craigs; Longformacus; near Greenlaw.
- F. fragillifolia* Tayl. R. Whitadder, on rocks by the old coppermine at Elba.
- F. dilatata* (L.) Dum. On trees. Frequent.
- Anthoceros punctatus* L. Fields by Lintlaw Burn.

CORM AND BULB FORMATION IN PLANTS, WITH SPECIAL REFERENCE TO THE GRAMINEAE. By W. BURNS, C.I.E., D.Sc., F.R.S.E.

(Read 13th June 1946).

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INTRODUCTION.

The formation of corms and bulbs is a characteristic feature of certain plant groups, particularly some of the monocotyledonous Natural Orders, such as the Liliaceae, Amaryllidaceae and Iridaceae. Corms and bulbs are also found in many other sections of the plant world, though not with the same intensity of representation.

In the winter of 1944-45, when the writer was going over the specimens of the Gramineae in the Herbarium of the Royal Botanic Garden, Edinburgh, his attention was attracted by certain species which, in varying degree, showed corms or bulbs. These, along with relevant literature, were examined as to their morphology and geographical distribution. The Director of the Royal Botanic Gardens, Kew, also put certain herbarium specimens at the writer's disposal. A few species were grown from seed or corms and examined in the live state. Microscopical preparations were made of their corms or bulbs and some preliminary experiments carried out on factors affecting the development of these structures. In this paper are put together the results so far obtained in this investigation.

THE CORM AND BULB-FORMING GRASSES.

Hackel (16) drew attention to the occurrence of bulbs and corms in some grasses found in areas of dry climate. He also pointed out that grasses of such areas often had their lower internodes protected by coverings of old leaf-sheaths. To this type of covering he gave the name tunika (=tunic). The following is the list of grass species cited by him as having corms or bulbs (the tunic grasses being omitted);—

I. MEDITERRANEAN REGION.

- Phalaris caerulea* Desf.
- P. tuberosa* L. (*P. nodosa* L.)
- P. truncata* Guss.
- Phleum pratense* L. var. *nodosum* Gaud.
- Alopecurus bulbosus* L.
- A. macrostachys* Poir.
- Holcus lanatus* L. var. *tuberosus* Coss.
- Arrhenatherum avenaceum* Beauv. var. *nodosum* Parl.
- A. avenaceum* Beauv. β *palaestinum* Boiss.
- A. avenaceum* Beauv. γ *erianthum*.
- A. Kotschyi* Boiss.
- Poa trivialis* L. var. *silvicola* Guss.
- Hordeum bulbosum* L.
- Poa bulbosa* L.
- Festuca spadicea* L.
- F. caerulea* Desf.
- F. triflora* Desf.

II. STEPPE REGIONS.

- Beckmannia eruciformis* Host.
- Colpodium bulbosum* Trin.
- Poa bulbosa* L.
- P. sinica* Steud.
- P. Reuteriana* Boiss. et Buhse.

III. SOUTH AFRICA.

- Ehrharta mnematea* L. fil.
- E. aemula* Schrad.
- E. Trochera* Steud.
- E. varicosa* Nees.
- E. ottonis* Kunth.

IV. AUSTRALIA.

Poa nodosa Nees.

V. CALIFORNIA AND PLATEAUX OF WEST U.S.A.

Melica bulbosa Gey.

M. californica Scribn.

M. spectabilis Scribn.

M. fugax Bol.

M. bromoides Gray.

M. subulata Scribn.

VI. HIGH PLATEAUX OF MEXICO.

Panicum bulbosum Kunth

P. scaberrimum Lag.

P. Torreyi Fourn.

DISTRIBUTION OF CORM- OR BULB-FORMING GENERA IN THE GRAMINEAE.

The distribution of corm- or bulb-forming genera among the tribes of the Gramineae shows the following pattern:—

Sub-family Pooideae.

Bambuseae	none
Phareae	none
Festuceae	<i>Poa</i>
	<i>Melica</i>
	<i>Molinia</i>
	<i>Festuca</i> (?) (see p. 333)
Aveneae	<i>Holcus</i>
	<i>Arrhenatherum</i>
Chlorideae	<i>Beckmannia</i>
Hordeae	<i>Hordeum</i>
Agrostidae	<i>Alopecurus</i>
	<i>Phleum</i>
Zoysiae	none
Phalaridae	<i>Ehrharta</i>
	<i>Phalaris</i>
Arundinelleae	none
Oryzeae	none

Sub-family Panicoideae

Melinideae	none
Paniceae	<i>Panicum</i>
Andropogoneae	none
Maydeae	none.

Only seven out of the fifteen tribes have corm- or bulb-forming genera. The position of these in Bews's diagram, indicating his hypothesis of the evolution of the Gramineae, is given in fig. 1.

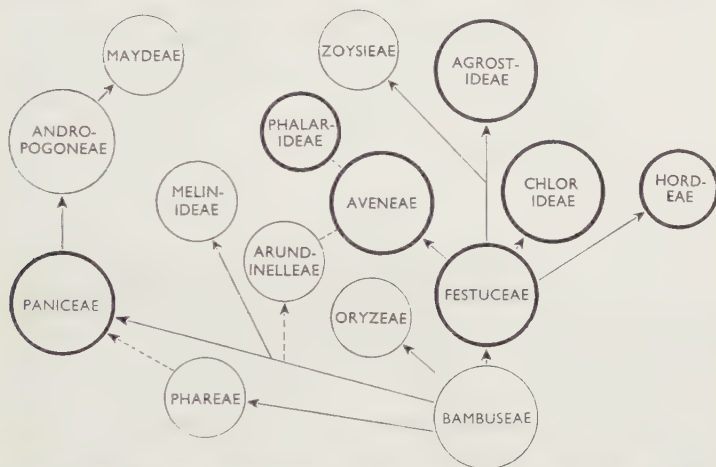


FIG. 1.—After Bews (*The World's Grasses*, p. 91). The tribes encircled with a heavy line are those containing corm- or bulb-forming species.

The primitive tribe of the Bambuseae does not have corms. In the sub-family Pooideae it would seem that the corm- or bulb-forming tendency came into being in the Festuceae and continued or re-appeared in the succeeding groups until the evolution of the Zoysiae, which show no such organs. In the Panicoideae the corm- and bulb-forming tendency is absent except for one* species (*Panicum bulbosum* Kunth). The great tribe of the Andropogoneae shows none. The naturalness of the two great sub-families Pooideae and Panicoideae has often been stressed. If absolutely no corm or bulb formation had been known in the Panicoideae this would have been taken as another proof of the marked cleft between these groups. The occurrence of this one corm-forming species in the Panicoideae brings up questions regarding the evolution of this feature which will be discussed later.

* Hackel (16) mentions three species, but two are doubtful (see p. 332).

CHARACTERS AND GEOGRAPHICAL DISTRIBUTION OF THE CORM- AND BULB-FORMING GRASSES.

In this section an attempt is made to put together the facts obtained from the examination, by the writer, of the Edinburgh and Kew herbarium specimens along with what has already been recorded concerning the species studied.

POA.

This widely distributed genus, so rich in forms, contains a group of species with true bulbs (*Poa bulbosa* L. and its allies), one species with single corms (*Poa nodosa* Nees) and one species with chains of slightly swollen internodes (*Poa trivialis* L. var. *silvicola* Guss.).

Poa bulbosa L. is well documented (e.g. Bews (8), Arber (5), S. F. Armstrong (3), and many Floras). Concerning it Bentham and Hooker state (7): "Remarkable for the bulbs formed by the swollen bases of the stems and the leafsheaths. . . . In dry waste places, on roadsides, etc., especially near the sea, in temperate and southern Europe and across Russian Asia, extending northwards into southern Scandinavia. In Britain chiefly near the sea, and only in the southern and eastern counties of England." The Field Club Flora of the Lothians, however, contains an entry to the effect that the species occurs at Musselburgh, Leith and Slateford, all near Edinburgh. J. M. Armstrong (2) states that *Poa bulbosa* was introduced from Europe into America and has become widely distributed. He draws attention to what he calls the bulblets which are formed in place of normal flowers (=bulbils). It is interesting that Bentham and Hooker neither describe nor figure these bulbils. Boissier (9) remarks concerning them: "Variet saepissime vivipara glumellis in gemmas foliaceas mutatis." In the herbarium specimens examined by the writer there were no bulbils on the specimens collected in Britain but they were present on many (though not on the majority) of the specimens collected in other parts of the world.

Aitchison (1), when with the Afghan Delimitation Commission in 1884-85, recorded *Poa bulbosa* as growing in great luxuriance over much of the area he traversed (i.e. at the junction of Afghanistan, Persia and Russian Turkestan, roughly between 61° and 63° longitude and 34° and 36° N. latitude). Two other corm-forming species were met with during his journey, viz. *Arrhenatherum Kotschyi*, which he describes as "an oat-like grass with curious bulbous roots", and *Geranium tuberosum* L. var. *Charlesii* Aitch. et Hemsl. The area in which Aitchison travelled has a long severe winter, a

damp and cold spring, and a short summer with great heat. There is no dewfall under 3500 ft. Winds, both hot and cold, are severe.

The British herbarium specimens examined by the writer came from Brighton, Rye, Yarmouth and the Isle of Wight. The European specimens came from Bulgaria, Sicily, Serbia, Spain, Switzerland, Denmark, Corsica, Italy, the Balearic Islands, Germany, Hungary, Corfu, Greece. From Africa and the East specimens had been collected in Tripoli, Armenia, Palestine, the Lebanon, Syria, Iraq, Afghanistan, Baluchistan, Persia, Turkestan, China (Yangtze watershed), India (Himalayas 16,000 ft. and Jhelum valley). Among the habitats given, sandy and gravelly areas predominate. These herbarium specimens showed much variability, not only in the amount of bulbil formation, but in the degree of expression of the bulb character, in stature and in the shape and size of the panicle.

Poa sinaica Steud. is given by Hackel (16) as occurring from Arabia Petraea to Persia. The present writer has examined two herbarium specimens. The first, in which bulbs are scarcely visible, was from Arabia Petraea. The second, which had its lower nodes covered with a thick tunic concealing the bulb (if any), was from Mount St. Catherine, Sinai, at 2000 metres above sea-level. Both Blatter (11) and Boissier (9) give this locality as the place of collection. The latter author says of the species "*culmis elatis bulbiformi incrassatis*" and says that there are small floral differences between this species and *Poa concinna*.

Poa Reuteriana Boiss. et Buhse was examined by the writer as one specimen from Kew. It is very like *Poa sinaica*, but with longer leaves and more flowers in the spikelet. Its habitat is in the Persian mountains.

Feinbrun (14) has recently dealt with the Palestine species of *Poa* which come under the Series *Bulbosae* of Roshevitz. These, according to her, are *P. bulbosa* L.; *P. Hackeli* Post; *P. Eigii* (sp. nov. Feinbrun); *P. sinaica* Steud. and *P. Timoleontis* Heldr. These differ in minor botanical characters and in geographical range. She also records that *P. Timoleontis* often grows in community with *P. bulbosa*. It would seem that this series of *Poas* is more than ready for exact study by means of cultivation experiments and cytological analysis.

Corm-forming Poas.

Poa nodosa Nees: In contrast to *Poa bulbosa*, which has a true bulb composed of thickened leaf bases, *Poa nodosa* has a true corm,

sometimes more than one. The herbarium specimens examined were all from South or West Australia. Bentham, in *Flora Australensis* 1878, vii, says of this species: "Stems usually about two feet high, forming at the base one, two or three superposed globular or ovoid nodules, three or four lines in diameter. . . ."

Poa trivialis L. var. *silvicola* Guss: This species is remarkable for the thickening of a whole series of basal internodes, giving a rosary effect. Hackel (16) points out that this character exists in all degrees of expression. The same is stated by Adr. Fiori in a label (in Italian) on an Edinburgh herbarium specimen collected near Vallombrosa in 1907. A herbarium specimen from Kew was from dried-out ditches and from meadows at Pola. Fiora, in a discussion (on the printed label of the first-mentioned specimen), expresses the view that the corm-forming character finds its full expression only in the Mediterranean area and that *silvicola* may therefore be regarded as a geographical race of *P. trivialis*. He also says that this does not exclude the possibility of the existence, side by side in the same place, of *Poa trivialis* proper and its variety *silvicola*.

MELICA.

In this genus we find a group of corm-forming species occupying a well-defined geographical area in Western America and Canada, some going as far north as Alaska and some as far south as Chile. Bews (8) remarks that this genus has many species which occur in the Mediterranean region, in S. Africa and other sclerophyllous regions where they mix with the *Macchia* shrubs. He adds that some produce corms and are known as onion-grass. The following are the corm-forming species:—

Melica bulbosa Gey.: The herbarium specimens examined by the writer came from Idaho (moist sunny hillsides at 6700 ft.); also from collections made in the exploration of Montana and Yellowstone Park (at 6000 and 6900 ft.); Colorado, Wyoming (6000 ft.) and E. Oregon. Hitchcock gives the habitat as rocky woods and hills, and the geographical area as Montana to British Columbia and California, also Jeff Davis County in Texas. The herbarium specimens showed one ovoid corm each, with the exception of one specimen which had two corms. Most of them also had a tunic.

Melica californica Scribn.: Hackel gives this as from California only. Hitchcock gives it as from California and from Oregon (Malheur county). The herbarium specimens examined by the writer were from California, and showed vertical rhizomes with

constrictions rather than true corms. Hitchcock says that the base of the culms is usually decumbent and more or less bulbous.

Melica spectabilis Scribn.: Hitchcock (21) shows this as being found in the same States as *M. bulbosa* Gey. and gives its habitat as rocky or open woods or thickets. The herbarium specimens examined came from the Yellowstone Park, Wyoming, East Oregon and Montana. This species has a corm system consisting of a loosely branched cord-like rhizome with corms at intervals (fig. 6).

Melica fugax Bolander: Hitchcock (21) calls it Little Onion Grass and says it is found from Washington to Nevada and central California on dry hills and in open woods. The herbarium specimens (from E. Oregon) showed well-marked corms and the species was marked "rare".

Melica bromoides Gray: The Kew herbarium specimen examined by the writer has pencilled on it "= *Melica Geyeri* Munro". Regarding *M. Geyeri* Munro, Hitchcock (20) remarks that it is bulbous at the base and occupies dry woods and rocky slopes at medium altitudes from western Oregon to central California and is found in the Yellowstone Park. The herbarium specimens examined were from California. They had broad leaves and well-marked tunics covering the corms.

Melica subulata Scribn.: Hitchcock calls it Alaska Onion Grass and gives its territory as from Western Wyoming and Montana north to Alaska and south in the mountains to California and to Chile. The herbarium specimens examined came from N. Idaho, California (at 1559 metres, scattered in low woods), E. Oregon (in the S. Canyon, on basaltic soil, west slope of the Blue Mountains) and the Aleutian Islands. In these specimens the degree of expression of the corm character varies, from merely incipient corms, through a stage which may be called rhizome-plus-corm, to single ovoid corms.

A herbarium specimen of *Melica acuminata* Bolander from Nevada (6000 ft.) showed a trace of corms.

In Canada MacCoun (27) reported *M. bulbosa* as occurring in the Rocky Mountains and British Columbia, *M. spectabilis* from a mountain valley north of the Thompson River and *M. acuminata* from various places, including Vancouver Island and Alaska.

Melicas which do not form Corms.

There are many areas in the Old World where corm-forming grasses are found but in which the *Melica* species produce none.

For example, there is a group of *Melicas* in the Caucasus (*minor* Hack., *nutans* L., *picta* C. Koch, *uniflora* Retz., *altissima* L., *ciliata* L., *micrantha* Boiss.). There is also the species *Melica Cupani* Guss. distributed in the Mediterranean region and as far east as the Himalayas. It was collected by Schimper on Mount Catherine,

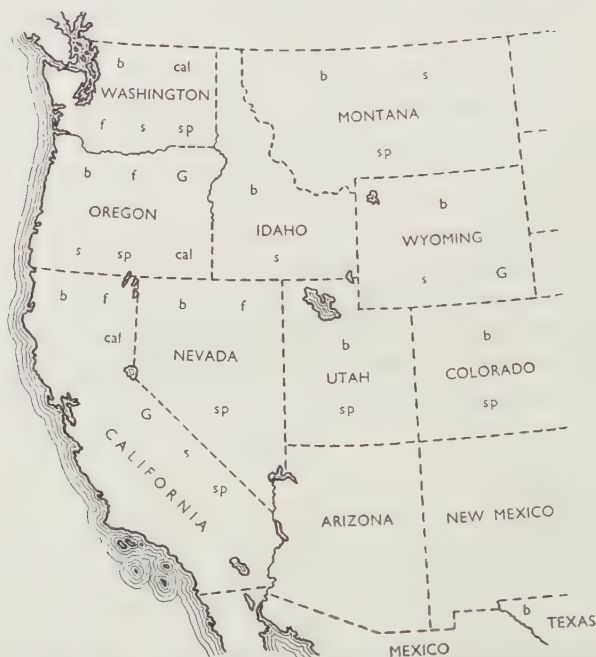


FIG. 2. Distribution of corm-forming *Melica* species in the Western States of the U.S.A. (b = *Melica bulbosa*; cal = *M. californica*; f = *M. fugax*; G = *M. Geyeri*; s = *M. subulata*; sp = *M. spectabilis*).

Sinai, where bulb-forming Poas are found. None of the above-mentioned *Melicas* show corms. The western American group of corm-forming *Melicas* therefore demands special interpretation.

The map (fig. 2) is a composite map made up from the small maps and information contained in Hitchcock's Manual (21) and shows the distribution of the corm-forming *Melicas* in the U.S.A. Alaska has not been shown. The corm-forming *Melicas* found in Alaska are *M. subulata* and *M. acuminata* (if the latter can be classed as corm-forming).

MOLINIA.

Molinia caerulea Moench.: This grass, not mentioned by Hackel (16), is often dominant in moorland. It has been described as to its

external morphology and anatomy in detail by Arber (5) and by Jefferies (23). It has a swollen internode, shaped like an Indian club, at the base of the culm. This internode is from 5 to 10 cm. long. Buds occur at its base and, beside it, a shrunk Indian-club internode (the lower end of last year's inflorescence axis) is often traceable. As to its anatomy and cell contents, Jefferies states that a transverse section of the swollen internode shows a small-celled cutinised epidermis, strengthened by a small-celled thick-walled mechanical tissue about three cells deep. The cortex is about ten cells deep, the walls thickened with cellulose and their cavities crowded with granules. The endodermis is inconspicuous. The pericycle is clear and is followed by a broad ring of sclerenchyma with vascular bundles having abundant thick-walled wooded elements. There are vascular bundles in an irregular double ring within the sclerenchyma zone and none in the centre. Microscopic preparations made by the present writer confirm these observations. The biological significance of these Indian-club-like structures is discussed later (p. 334).

COLPODIUM.

Colpodium bulbosum Trin.: Hackel (16) mentions this as from S. Russia, Armenia and Persia. The specimen examined was from the Caucasus and has small tubers, in tufts, with fibrous tunics. The same structures were seen in *Colpodium parviflora* Boiss. et Buhse (a specimen from north Persia). *Colpodium humile* Griseb. showed small but definite tubers. *Colpodium violaceum* Griseb. showed very little basal swelling.

It seems not unlikely that here, as in the bulbous Poas, we have a series of forms that require study by the methods of experimental cultivation and cytological analysis. These Colpodiums seem to prefer sandy soil and are found from the shores of the Caspian up to 6000 ft. in the Persian mountains and the Caucasus.

HOLCUS.

In this genus there is one variety of one species which shows corm formation. This is *Holcus lanatus* L. var. *tuberosus* Coss. (*Holcus tuberosus* Salzm.). Hackel (16) gives its distribution as in Algeria, Morocco and southern Spain; Willkomm (39) reports it from the coastal area between Almeria and Gibraltar (S. Spain) with sandy soil as its habitat. The two herbarium specimens examined were from Algeria. One of these was incomplete. The other had swollen lower nodes of the size of peas, arranged hori-

zontally, *i.e.* each at the base of an ascending culm from a sympodial system. In the "Flore d'Alger" it is stated that the lower internodes are swollen and that the plant occurs amongst scrub. The authors of that Flora (Battandier and Trabut) consider this a polymorphous species and opine that *Holcus argenteus* l'Agardh and *H. Reuteri* Boiss. may also be referred to it. Herbarium specimens of these two species do *not* show corms.

ARRHENATHERUM.

Arrhenatherum avenaceum Beauv. var. *nodosum* Parl. (*Avena nodosa* L.) is, at least in Britain, the best known of the corm-forming grasses, since it is a troublesome weed. It has been often described (*e.g.* S. F. Armstrong (3), Arber (5)). Several of the basal internodes of each culm become swollen, forming a row of corms. There are forms of this species which produce no corms, some which are markedly corm-forming and others which are intermediate (Jenkins (24)). The herbarium specimens examined showed such a range of forms. The writer also grew two cultures, one of a corm-forming type and the other of a type without corms. Both remained constant to their types. The range of this species is wide. It grows throughout Europe. It is found in Algeria, Morocco and Kurdistan. It is not indigenous to North America or Australia. It can live at moderate altitudes and has been reported from 5000 ft. in Armenia.

Arrhenatherum avenaceum Beauv. β *palaestinum* Boiss.: Boissier (9) gives its range as Rhodes, Palestine and Mesopotamia. Hackel adds Crete and Phrygia. The herbarium specimen examined by the writer had one relatively large corm (12 mm. each way) and two smaller corms attached to it on one side. This sheet, which was from the Hebrew University of Jerusalem, had on it the following note:—

"Phytogeographic value: a species of the sub-Eastern-Mediterranean element, penetrating into the Irano-Turanian region. Its ecological requirements in Palestine are obviously Mediterranean. Its penetration into Mesopotamia (Irano-Turanian territory) is certainly connected with the Mediterranean enclaves in the mountains of North Mesopotamia. It is a component of open Mediterranean associations, *e.g.* *Poterietum spinosi*. *Arrhenatherum palaestinum* is limited in Palestine to the Mediterranean mountain districts where it is rather a rare plant. Jerusalem. Mt. Scopus 15, iv, 1931. Leg. Zohary and Jahlom".

This variety is given in the Balkan Prodrômus as occurring in Greece, Macedonia and Thessaly, but no mention is made of corms. The species is not one of those described in "Flore d'Alger".

Arrhenatherum avenaceum Beauv. γ *erianthum* (*Avena erianthum* Boiss. et Reut.): The herbarium specimens were all from rocky calcareous areas in Spain and described as rare. The species appears to be endemic to Spain. The corms were of the size of peas. The Balkan Prodrômus (19) gives it as synonymous with *Avena hispanica* Lange. The entry regarding corms reads: "nodis infimis saepe tuberoso-incrassatis".

Arrhenatherum Kotschyi Boiss.: Hackel gives it as being found in Persia, Kurdistan and Syria. Boissier (9) says it is perennial, with superimposed corms, and inhabits rocky and shady mountain areas. He also remarks that it differs from *palaestinum* by certain floral characters. Aitchison (1) recorded it from Khorasan in moist soil, near water, at an altitude of 5000 ft.

BECKMANNIA.

Beckmannia eruciformis Host.: This is a grass of swamps and sloughs, found in Europe, Asia and America. Hackel considered its main area to be central and south Russia, Siberia and north China. From this area it extends (according to him) on the one side to Greece, Italy, Hungary and Rumania, and on the other to Japan and to the U.S.A. (California, Colorado and Washington). He states that its tuberous thickening is not constant. This remark is borne out by the herbarium sheets examined. Only one herbarium specimen (collected in Achaia, Greece) had unmistakable corms. These were about 12 mm. long and 8 mm. across.

HORDEUM.

Hordeum bulbosum L.: Rikli (31) mentions this species as a well-known Mediterranean grass. Nikitin (29) says it is a typical representative of the Mediterranean flora and, in the Soviet Union, is found in the Crimea and Transcaucasia. It also occurs in central Asia. Outside the U.S.S.R., according to the same writer, its distribution is extensive in Asia Minor, Turkish Armenia, Kurdistan, North Iran and the Balkan Peninsula. It appears to be semi-domesticated as a hay-producing plant among the hills and valleys of Kopet-Dag. It appears also as a weed of irrigated wheat land in the vicinity of Geok-Tepe. The herbarium specimens examined

came from the Caucasus, Greece, the Dardanelles, Dalmatia, Persia, Serbia, Smyrna, the Lebanon, Rhodes, Algeciras (in the maquis), Sicily, Cyrenaica and Tangiers. The corm is a marked feature of this plant and measures about 15 mm. each way.

Hordeum violaceum Boiss. et Huet: Boissier (9) gives this as occurring in mountainous areas of Armenia, the Caucasus and Persia. Hackel does not mention this species as one that forms corms. The herbarium specimens examined have the lower internodes slightly swollen but do not possess the marked corms of *H. bulbosum*, though occurring in many of the areas where *H. bulbosum* is found.

Aitchison (1), when with the Afghan Delimitation Commission, came across great areas of *Hordeum ithaburense* which "was in such profusion and so much resembled cultivated fields that my followers called it wild barley, an opinion shared by most of us". This species has no corms, though occurring in an area where one would expect corm formation and in which Aitchison had already found *Poa bulbosa*, *Arrhenatherum Kotschyi* and *Geranium tuberosum*.

ALOPECURUS.

Alopecurus bulbosus Gouan: Bentham and Hooker (7), dealing with *Alopecurus geniculatus* L., remark that in some localities, especially near the sea, the stem thickens into "a kind of bulb", which state has been distinguished as a species under the name of *A. bulbosus* Gouan. S. F. Armstrong (3) says this form is rare. The herbarium specimens examined bear out Bentham and Hooker's remarks as to habitat. They came from the tidal Avon at Shirehampton, salt marshes at Lodmoor (Weymouth) and Brading Harbour (Isle of Wight). From the last-named place the typical non-corm-forming *A. geniculatus* L. was also collected.

In Algeria is found *Alopecurus bulbosus* Linn. given in "Flore d'Alger" as synonymous with *A. macrostachys* Poir. Algeria is also the only locality mentioned by Hackel (16) for *Alopecurus macrostachys* Poir., and the one herbarium specimen examined was also from Algeria. Rikli (31) mentions *A. bulbosus* (without stating whether of Gouan or Linnaeus) as a common Mediterranean plant.

PHLEUM.

Phleum pratense L., the well-known timothy grass, has a swollen lower internode to which Evans (13) has given the name haplocorm.

The degree of swelling of this internode varies considerably. The internode above this haplocorm is usually also solid. Innovation buds arise from the nodes above and below the haplocorm. The haplocorm is by no means the lowest node of all. There is a series

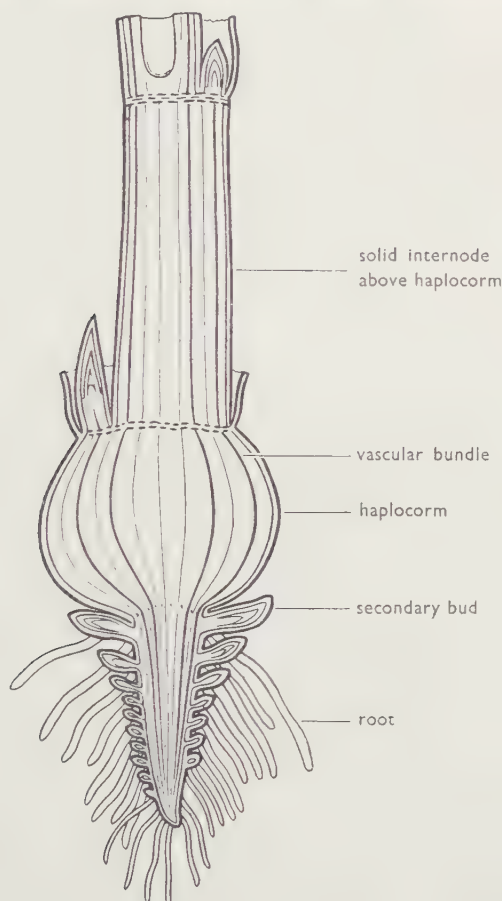


FIG. 3.—Longitudinal section of base of culm of *Phleum pratense* L.
(after Nishimura, Japanese Journal of Botany, I, 55, Pl. V).

of telescoped internodes below it (fig. 3). The biological significance of this swollen internode is dealt with later (p. 334).

Gregor and Sansome (15) divide the species, as found in Britain, into two apparently inter-sterile groups. Group I they call "American", which includes types that are constantly found in agricultural samples from America and Europe. Group II is termed "British Wild" and contains multi-tillering low-growing types. In

Group I the fertile stems are strong, and may have one, two or even three swollen internodes. Haplocorms may not be present on all stems of a plant. This type (Group I) is seldom, if ever, common in old closely grazed pastures. In Group II the fertile stems are slender and haplocorms are often poorly developed, while in some plants they are completely absent. The authors found, in a waste place, a much dwarfed plant with well-developed haplocorms. At the time, this plant was identified as *P. pratense* var. *nodosum*. When grown in culture it assumed the habit of Group I and, on being selfed, yielded a population indistinguishable from the "American" Group. The cytological evidence confirmed this.

The cytological studies of these authors showed that Group I is hexaploid with $2n=42$, while Group II is diploid with $2n=14$. A very important point made by the authors is that within each group a relationship exists between the growth-forms of a particular habitat and the environmental conditions of that habitat. Both Groups possess similar growth-forms, with the exception that in Group I the prostrate form has not been found.

Among the herbarium specimens of the type hitherto known as *Phleum pratense* var. *nodosum*, examined by the present writer, were some that were dwarf but had marked haplocorms. One of these was from Arthur's Seat in Edinburgh. Another was from the Heughs of St. Cyrus. This is a rocky scarp facing the North Sea and well known as a sanctuary for several species. Herbarium specimens from Spain, Switzerland and Italy showed well-marked haplocorms, sometimes in masses. Gregor and Sansome (15) consider that the varietal name *nodosum* is superfluous and serves no useful purpose in the classification of British material. Other *Phleum* species do not show haplocorms.

EHRHARTA.

After eliminating synonymous species we have definitely three corm-forming species (all South African):—

Ehrharta Capensis Thunb.: The herbarium specimens examined show well-marked corms joined by short or long cord-like rhizome connections. The species prefers sandy soil, and many coastal areas are cited in *Flora Capensis* as its habitat.

Ehrharta bulbosa Sm.: This species is also found in coastal areas and normally has the lowest internode swollen.

Ehrharta longifolia Schrad.: Of the three herbarium specimens examined, two had big corms with a finely pitted surface; the third

specimen had less marked swellings. *Flora Capensis* gives this species as perennial, with a more or less tuberous base, and its habitat also coastal. The specimens examined were labelled as from Stellenbosch Flats, Table Mountain and a waterfall at 1200 ft. above sea-level.

Among other S. African *Ehrhartas*, not mentioned by Hackel (16), but examined by the writer (as herbarium specimens), the following show indications of corms: *E. barbinoides* Nees; *E. gigantea* Sw., *E. longiflora* Sw., *E. melicoides* Sw. Stapf (33) describes a variety (*a stenophylla* Stapf) of *E. gigantea* as "sub-bulbous", and *E. melicoides* as having "an almost bulbous thickening at the base". *E. tetarrhena* (West Australia) has definitely swollen lower internodes.

PHALARIS.

Phalaris caerulea Desf.: In "Flore d'Alger" (6) it is stated that this species differs from *Ph. bulbosa* L. in certain small characters of the spikelet, and from *Ph. minor* Retz. in its knotty perennial rhizome. The same publication indicates that its habitat is in pastures and the edges of fields and that its geographical area is the western part of the Mediterranean region and the Canary Islands. In the *Balkan Prodromus* (19) it is stated that the basal internodes are thickened and that the species occurs in damp places in the Mediterranean region. The Kew herbarium specimens examined by the writer had been collected on the Sierra de Monsanto, Portugal, and one of them showed two swollen internodes.

Phalaris truncata Guss.: It would seem that this species is not possessed of corms. The *Balkan Prodromus* states this definitely. "Flore d'Alger" makes no mention of corms. The Kew herbarium specimen examined showed none. Boissier (9) remarks: "Differt a *Ph. nodosa* caudice incrassato caespitoso et caulibus basi non nodosis. . . ." It is found on both the European and African sides of the Mediterranean, and specimens are recorded from (among other places) Algeria, South Italy and Sicily.

Phalaris minor Retz.: Concerning this species it is remarked in *Conspectus Florae Graecae*, "culmo basi vix incrassati". This "incipience" of thickening was noticeable on two herbarium specimens, one from Capri and the other from Baluchistan. This species is a native of the Mediterranean area and is also found in South Africa and in America, particularly in California, where it has been introduced from the Mediterranean region. The species being annual, a storage organ would not seem to be a biological necessity.

Phalaris tuberosa L. (*Ph. nodosa* L., *Ph. bulbosa* L.). Boissier (9) states that one to four internodes may be thickened in a moniliform manner and that the geographical area of the species comprises the European and African countries of the Mediterranean and the Canary Islands. The moniliform basal portion is also described in *Conspectus Florae Graecae*. Bews (8) remarks: "*Phalaris tuberosa* L. (*Ph. bulbosa* L.) Toowoomba Canary Grass, is a native of the Mediterranean region but is now extensively cultivated in Australia, Africa, N. America and elsewhere." Toowoomba Canary Grass is so named because it was distributed from the Botanic Garden, Toowoomba, Queensland about 1907. It appears to be a survival and probably a mutant from seed imported about 1888 into Australia from the U.S.A. Hackel described it as a distinct species (*Ph. stenoptera*). Stapf identified it as *Ph. bulbosa* L. Hitchcock (21) gives it as *Phalaris tuberosa* L. var. *stenoptera* (Hack.) Hitchc. and states that it differs from the typical *Ph. tuberosa* of the Mediterranean region in having short vertical or ascending, sometimes branching, rhizomes, the base of the culms being little or not at all swollen.

The present writer grew plants from seed labelled *Phalaris bulbosa* and kindly sent in 1945 by the Waite Agricultural Research Institute, Adelaide, S. Australia. These plants correspond to Hitchcock's description. The bases of the culms are only slightly swollen and there are no chains of corms. The herbarium specimens from the Mediterranean area, on the other hand, do show such moniliform internodes. They came from Morocco, Palestine, Algeria (coastal marshes) Kurdistan (lower slopes of Kuh-Sefm on the district of Erbil) Tunis and Teneriffe, Athens and Rhodes. The Tunis and Teneriffe specimens both showed chains of relatively large corms.

PANICUM.

Panicum bulbosum Kunth is the only species we have to consider. Of the other two mentioned by Hackel (16), *P. scaberrimum* is given by Hitchcock and Chase (20) as a synonym of *P. maximum* (which has no corms). Regarding *P. Torreyi*, Hitchcock and Chase (20) state that the specimen in the Fournier Herbarium cited by Fournier under this name is *P. bulbosum* L. For the rest they find *P. Torreyi* Fourn. in Hemsl. Biol. Centr. Americ. Bot., 3, 497, 1885. to be synonymous with *P. philadelphicum* Bern. which has no corms.

In *P. bulbosum* L., however, the corms are marked. They are the lowest nodes of sympodially arising culms. Of the herbarium

specimens examined, certain ones from Mexico showed more rhizome than corm, the corms being just indicated, while the rhizome had thickened up. Another Mexican specimen, however, showed a relatively gigantic single corm. Hitchcock says the species occurs in moist places in canyons and valleys from West Texas to Arizona and in Mexico. The herbarium specimens examined were from New Mexico (6000 to 7500 ft.), Nevada (2000 to 3000 ft.), Arizona, and the Chiricahua Mountains (8000 ft.).

Species with Simulated Bulbosity.

There are some grass species which, at first sight, seem to have corms or bulb. On closer examination, one sees that the swollen base is due to other causes. *Schmidtia bulbosa* Stapf is described by Stapf in Dyer, Fl. Cap. vol. 7, 658, as having "numerous villous conical innovation buds at the base (base hence more or less bulbous)". The present writer dissected the bulbous base and found an upright thin rhizome with innovation buds, leaf bases and root initials arising from it. *Bromus variegatus* Bieb. is rather like *Schmidtia* in this respect. *Eragrostis eriopoda* Benth. and *E. laniflora* Benth. have felted hairs on the short basal cataphylls, giving the base a bulbous appearance as noted by Hackel (16). The three *Festucas* mentioned by Hackel all show marked tunics, that of *F. caerulascens* being peculiarly fibrous. None of them, however, have true corms or bulbs and the swollen base is due to the innovation-buds and slight thickening of the leaf sheaths. *F. spadicea* has, however, a curious positively geotropic rhizome (Arber (5), p. 272, fig. 137).

THE BIOLOGICAL SIGNIFICANCE OF CORMS AND BULBS.

Hackel (16) was of opinion that the main function of the grass corms and bulbs must be water storage, particularly for the benefit of the young shoots which develop from buds at the base of the swollen internodes. He also thought it possible that the water supply of the leaves might be regulated from these storage organs. He hoped someone would, in the Mediterranean area, conduct experiments to find out whether there are marked differences in the turgor of corms and bulbs in the early morning and after a hot afternoon. He considered it would be interesting to run parallel cultures, in such conditions, of the corm-forming and non-corm-forming varieties of *Phleum pratense* and *Arrhenatherum avenaceum*, and see which stood up to drought better. Such experiments have

not so far been carried out. Hackel also found that a copiously watered plant of *Poa bulbosa* (grown in a pot from a bulbil) showed little sign of a bulb.

Evans (13) hazards a guess that the haplocorm of timothy contains a store of nutrients for the growth of innovation buds during the summer months or even for transference to the seed. The authors of the University of Missouri Agricultural Research Bulletin 19 are strongly of opinion, based on experiments, that the function of haplocorms is to give an early start and vigorous growth in the year following their formation. Hence late cutting for hay is an advantage, as it means well-ripened haplocorms. Nishimura (30), on the basis of field experiments and microscopical and chemical examination of the contents of the haplocorm, is of a similar opinion, *i.e.*, that the haplocorm is specially concerned with the development of the shoots of the following year. After these shoots have used up the reserve material the haplocorm disintegrates.

Similar conclusions have been reached from observations on other corm-forming grasses and on tuberous plants of other Natural Orders. Jefferies (23), dealing with the Indian-club-like internode at the base of the culm in *Molinia caerulea*, considers that it is a storage organ and gives the plant an early start to growth in the spring. He points out, however, that such an early start may expose the new foliage to frost. In excessively cold springs etiolation of the new foliage in this species is so abundant that wide stretches of it look yellow. Woodhead (40) dealing with the comparative ecology of bracken (*Pteris aquilina* L.), bluebell (*Scilla festalis*) and *Holcus mollis* L. states that the *Scilla*, with its deeply set bulb, is the first to make its appearance, and is exposed to the danger of frost, but possesses an almost unfreezable sap. Huxley (22) compares the difference in winter habits of the common cuckoo-pint. *Arum maculatum* L., which overwinters as a deep-seated corm immune to most frosts and *Arum neglectum* which produces its new foliage in December. The latter is readily killed by frost, but, where it survives, its winter photosynthesis has resulted in much growth in spring before the trees have developed their leaves and shaded it. The British range of *Arum maculatum* extends far into Scotland, whereas *A. neglectum* is restricted to the south and south-west coasts of England. It may therefore be said that *Arum neglectum* shows an adaptation to woodland life but only in mild temperate climates. *Arum maculatum*, on the other hand, in its resting corm stage, escapes the frost that kills *A. neglectum*. Jenkin (24) considers that the extreme tuberous type of *Arrhenatherum*

avenaceum depends entirely on the corms for carrying on over the winter. It may thus be smothered out by grasses having winter growth, e.g. *Poa trivialis* and species of *Agrostis*. The non-corm-forming *Arrhenatherum* might be grazed out of existence in the winter. He thinks the forms intermediate as to corm-formation would stand the best chances of survival.

The present writer had grown plants of both corm-forming and non-corm-forming *Arrhenatherum avenaceum* in an experimental plot, and both had done well in the summer of 1945. In the spring of 1946 there was a late frost with much wind. The corm-forming plants survived but the non-corm-forming plants were killed.

Kirchner and Volkart (25) point out that most grasses do not have a resting season. Exceptions are certain grasses from areas of either physical or physiological drought (including some swamp grasses). Many grasses are green throughout comparatively severe winters and are therefore able to encroach on territory left vacant by other plants. In areas of intense cold, with no snow cover, grasses may, however, enter into a period of winter rest. Such grasses always have storage arrangements in sheathing leaves, roots, rhizomes or other organs. The authors state that reserve materials in such organs were for a long time overlooked, as they are often carried in solution or in a colloidal state in the cell-sap. Such materials are graminin ($C_{48}H_{80}O_{40}$), phlein ($C_{90}H_{150}O_{75}$) and triticein ($C_{30}H_{50}O_{25}$). They state that all three are closely related to the sinistrin of the Liliaceae and the irisin found in the rhizomes of *Iris pseudacorus*. The three first carbohydrates mentioned are, according to the authors, present in noticeable quantities (5 to 10 per cent.). These carbohydrates are easily turned into sugar and so enable the grasses to resume growth quickly during frost-free periods in the winter and, later on, in the spring.

Arber (5) describes large sphaerocrystals which she thinks were probably of phlein in a section of the haplocorm of *Phleum pratense* stained with methyl green and examined in dilute glycerin. Storage of reserve carbohydrate as reserve cellulose occurs in *Poa bulbosa* (Arber (5), p. 273, fig. 138) and in *Molinia caerulea* (Arber (5), p. 141, fig. 277) (also Jefferies (23)). In *Molinia*, according to Arber, the cells of the ground tissue of the Indian-club-like internode are at first full of minute starch granules and protein grains. Later the starch is dissolved and the carbohydrate is laid down as reserve cellulose in the walls of the ground tissue. In both *Poa bulbosa* and *Molinia caerulea* this reserve cellulose is at its maximum in the autumn.

Kirchner and Volkart (25) have not dealt specially with resting periods enforced by xerophytic conditions, but the reasoning would seem to apply there also. An important point is made by Maksimov (28). He has demonstrated that drought stops growth even more than it stops photosynthesis, the products of which, in consequence, accumulate. More recently Lubimenko (26) has shown that, in some circumstances, there is an increase in photosynthesis after partial dehydration of the leaf. Accumulating products must be stored somewhere. If the above-ground parts are dying, the parts at or below the surface must receive the material and become storage organs. Apart from certain cases like the cord roots of *Molinia*, the fibrous roots of the grasses are not suitable for storage organs and hence it is natural that the rhizomes, the lowest nodes of the stem, or the bases of sheathing leaves should become such organs.

Rikli (31), dealing with geophytes in the Mediterranean region, stresses the fact that these plants, at the onset of the dry season, lose their transpiring parts, and that all usable plastic material is withdrawn into subterranean organs in the form of various carbohydrates. Sclerenchymatous tissue and tunics protect these organs from the pressure and movement of the drying soil. The author later points out that tuber formation takes place in a great number of Natural Orders throughout the Dicotyledons, mainly of the Mediterranean area, but that in no one Order or even genus are corms widely present. He then gives the following list:

NATURAL ORDER.	CORM OR BULB-FORMING SPECIES.
Aristolochiaceae	<i>Aristolochia rotunda</i> , <i>cretica</i> , etc.
Polygonaceae	<i>Rumex tuberosus</i>
Ranunculaceae	<i>Ficaria</i> ; several <i>Anemones</i> (e.g. <i>coronaria</i> , <i>hortensis</i> , etc.), some <i>Ranunculus</i> species (<i>asiaticus</i> , <i>flabellatus</i> , etc.)
Papaveraceae	The genus <i>Corydalis</i> ; <i>Leontice leontopetalum</i>
Crassulaceae	<i>Sedum tuberosum</i>
Papilionaceae	<i>Lathyrus tuberosus</i>
Geraniaceae	<i>Geranium tuberosum</i>
Oxalidaceae	<i>Oxalis cernua</i>
Umbelliferae	<i>Bischolettia tuberosa</i> : the genera <i>Bulbo-</i> <i>castanum</i> , <i>Bunium</i> , <i>Butinia</i> , <i>Conopodium</i> , etc.

NATURAL ORDER.	CORM OR BULB-FORMING SPECIES.
Primulaceae	<i>Cyclamen</i> (both spring- and autumn-flowering types)
Solanaceae	<i>Mandragora autumnalis</i> and <i>officinarum</i>
Valerianaceae	<i>Valeriana dioscoridis</i> , <i>leucophlea</i> and <i>tuberosa</i>
Cucurbitaceae	<i>Bryonia</i> species
Compositae	<i>Scorzonera</i> ; <i>Crepis tuberosa</i> , <i>Thrinicia tuberosa</i> , <i>Tussilago farfara</i>

We may add to Rikli's list:

Ranunculaceae	<i>Ranunculus bulbosus</i> and <i>bullatus</i>
Umbelliferae	<i>Carum cylindricum</i> and <i>bulbocastanum</i>
Labiatae	<i>Nepeta tuberosa</i>
Euphorbiaceae	<i>Euphorbia tuberosa</i> (Africa)
Geraniaceae	<i>Geranium reflexum</i> <i>Pelargonium</i> species such as <i>Rodneyanum</i> (Africa)
Droseraceae	<i>Drosera rosulata</i> , <i>microphylla</i> , <i>macrophylla</i> , <i>macrantha</i> , <i>heterophylla</i> , <i>bulbosa</i> , etc. (W. and S.E. Australia)

Corms and bulbs are also found in the Cyperaceae and Juncaceae (see p. 343) of the Monocotyledons.

Those who doubt whether corm and bulb formation in the Gramineae is of the nature of an adaptation, because all the grasses in the area do not show these structures, may be referred to Huxley's (22) treatment (amounting almost to a castigation) of such questioners. He points out that there are, in fact, numerous possible explanations of such a state of affairs. Mutations in that direction may not have occurred or were not available before mutations in some other direction set the stock specializing along other lines. It may also be (according to him) that there are differences in the make-up or the environment of forms as yet undetected by us, which make such an adaptation more advantageous to one form than to another.

It is interesting to note that among the grass species or varieties dealt with in this paper there are cases of (1) the co-existence in the same area of what, in the present state of our knowledge, is considered the original non-tuberos type, side by side with its tuberos mutant (e.g. *Poa trivialis* L. and *Poa trivialis* L. var. *silvicola* Guss., *Alopecurus geniculatus* L. and *Alopecurus bulbosus* Gouan.); (2) the

existence in the same area of several allied bulbous or tuberous species (e.g. *Melica* species in America and *Ehrharta* species in Africa, *Poa bulbosa* and *Poa Timoleontis* in Palestine).

DEVELOPMENTAL MORPHOLOGY AND EVOLUTION OF CORMS AND BULBS.

Corm and Bulb Size, Shape, Arrangement and Anatomy.

All the grass corms examined are swollen internodes on the lower part of the culms. Sometimes only one internode is swollen (as in

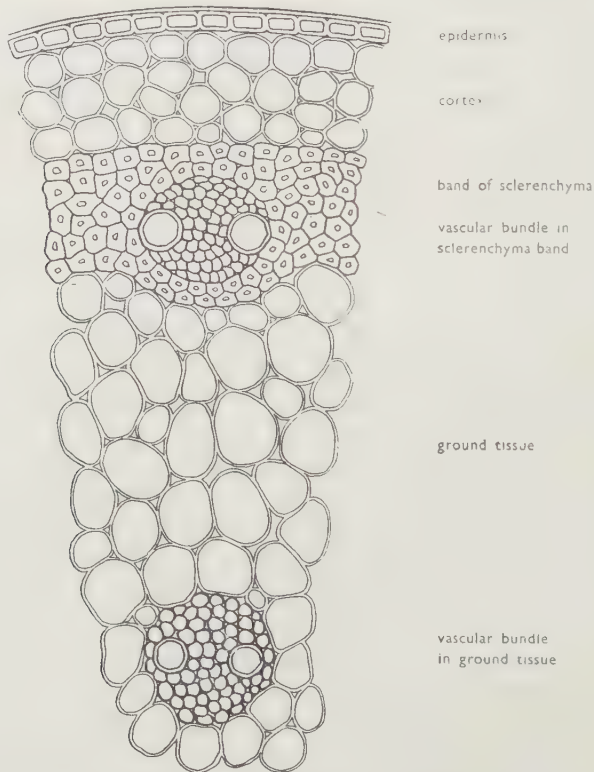


FIG. 4.—Transverse section of haplocorm of *Phleum pratense* L.

Hordeum bulbosum). Sometimes there is a chain of swollen internodes (as in *Arrhenatherum avenaceum* and *Poa trivialis* var. *silvicola*). There are frequent cases where a species, which typically produces one corm only, shows an additional one, or sometimes two, just above it (e.g. *Phleum pratense* and *Poa nodosa* (fig. 5)). The same kind of thing occurs in the dicotyledons (e.g. *Thrincia tuberosa*).

The shape of the grass corm may be nearly spherical (*Hordeum bulbosum*; *Ehrharta* species), barrel-shaped (*Poa trivialis* var. *silvicola*), ovoid (*Melica bulbosa*), onion-shaped (*Arrhenatherum avenaceum*) or shaped like an Indian club (*Molinia caerulea*). Corm size varies from about 5×7 mm. in *Poa trivialis* var. *silvicola* to 15×15 mm. in *Hordeum bulbosum*.

In one or two species such as *Melica spectabilis* (fig. 6) and *Ehrharta capensis* there is a corm system consisting of corms connected by rhizomatous cords. Grass corms often have the additional protec-



FIG. 5.—*Poa nodosa* Nees (specimen with two corms).

FIG. 6.—*Melica spectabilis* Scribn. (branched rhizome with corms = C).

tion of "tunics" (dead sheaths of old leaves) as in *Hordeum bulbosum*, *Melica bulbosa* and *Molinia caerulea*. Corm development may take place on all or most tillers.

Cross-sections of grass tubers examined show the following common characters (fig. 4):

- (1) A small-celled epidermis with a marked cuticle.
- (2) A cortex of two or three layers of cells.
- (3) A band of sclerenchyma with vascular bundles in it.
- (4) A central cylinder of fundamental tissue with larger vascular bundles, mainly toward the periphery and sometimes in two irregular rings.

Where bundles from innovation buds, sheathing leaves, or roots enter the corm there is a very confused cross-section.

Degree of Expression of the Corm- or Bulb-Forming Character.

The degree of expression of the corm- or bulb-forming character varies greatly. There are species (*e.g.* some *Ehrhartas*) which appear to be, figuratively, on the verge of corm formation, but, even in species which are definitely corm forming, there is much variation. Sometimes these species show well-developed corms, sometimes "incipient" corms and sometimes none. It is reasonable to assume that this is due to the interaction of varying genetic composition and varying environment. Huxley (22) is insistent on this point. He writes (p. 63):

"Any given character represents the end result of a great number of genes interacting with the environment during development and is not inherited as such. What is investigated in any genetic experiment is the inherited basis for a constant character difference. Thus a *character-difference* may be said to be inherited in Mendelian fashion, while a *character* cannot; but, even so, the differential effect of a particular gene on the particular character need not by any means be the same. It may alter according to differences in environment and also according to differences in the remainder of the gene complex. As an example of the first we may take the well-worked-out case of 'abnormal abdomen' in *Drosophila* (T. H. Morgan, 1915). This effect depends on a single partially dominant sex-linked gene, but it is only manifested in moist conditions. In dry conditions, flies pure for the gene appear perfectly normal, while intermediates are produced by varying degrees of moisture. . . . An equally striking botanical case is that of a type of albinism in barley (Collins, 1927) dependent on a single gene. When grown below 6.5° C. the plants entirely lack chlorophyll, while above 18° C. they are quite normal. Between these limits they produce a graded amount of chlorophyll."

The present writer would cite, as another botanical case, the character of swollen petiole, which is the floating apparatus of the water hyacinth (*Eichhornia crassipes*). If this plant is grown on land in a flower-pot, it loses this swelling, and all intermediate stages can be obtained.

Variation in the expression of the corm or bulb character is indicated in the language of many of the Floras. We find for example such phrases as "*culmis erectis saepe bulbiformi incrassatis*" (Boissier, *Flora Orientalis*, 1884, p. 605 re *Poa bulbosa*); "the base usually decumbent, more or less bulbous" (Hitchcock, "Manual of the Grasses of the U.S.A.," re *Melica californica*).

What, then, is the environment in which the corm- or bulb-forming character finds its fullest expression? Hackel (16) from observations made on his travels, was of opinion that corm-producing individuals of *Phleum pratense* were far more common in the Mediterranean area than in mid-Europe and that the same applied to *Alopecurus bulbosus*. In addition to these *Arrhenatherum avenaceum* and *Festuca spadicea* (but see p. 333) were the only corm-forming, and *Poa bulbosa* the only bulb-forming, species in mid-Europe. All these were far more common in the Mediterranean region, which had in addition many species (with corms or bulbs) not found in mid-Europe. Hackel's belief, that the Mediterranean region is the place *par excellence* for corm- and bulb-forming grasses has been borne out, as we have seen, by the places of origin of the herbarium specimens examined. Not only so, but areas in other parts of the world with the so-called Mediterranean climate (areas of winter rain and hot summers) have a similar vegetation including corm- and bulb-forming grasses. These may be found in areas still more xerophytic, such as steppe or semi-desert, also at medium to high altitudes in certain mountain regions, and occasionally in swamp conditions, always provided there is a dry season enforcing a period of vegetative rest. A few have been able to invade and hold their own in other places but, generally speaking, corm- and bulb-formation is characteristic of areas of Mediterranean climate.

The Mediterranean Climate.

Hardy (18) defines this region around the Mediterranean itself as follows:

"The region of warm temperate climate, with a mild and rainy winter and a hot dry summer, is fairly well defined geographically round the shores of the Mediterranean by a barrier of mountains and highlands: the Pyrenees, the central plateau of France, the Alps and the Rhodope range. On the east the Mediterranean region is bounded by the Anatolian plateau, the Taurus, and the Syrian desert; on the south it embraces broken strips of the North African headlands such as the coast of Cyrenaica, a coast strip of Tunis and the Tell of Algeria and Morocco north of the Atlas. On such a vast and diversified area the climate naturally changes in its details but remains fairly constant in its typical features. . . . Bulbs and tubers and rootstocks are characteristic of this region."

As to the areas with similar climate in other parts of the world the same writer remarks:

"Thus the vegetation of the Mediterranean scenery all over the world is singularly alike, whether the Mediterranean of the Old World, California, the central valley of Chile, the south-west corner of Africa, or the south-west corner of Australia be considered."

Huxley (22) points out that the study of faunas and floras confined to particular habitats will invariably reveal certain recurrent peculiarities and that frequently we can deduce an animal's mode of life from the structural adaptation which it possesses. Occasionally (he says) we may be puzzled, but find that fuller knowledge solves the puzzle. Scott-Elliot (32), dealing with the Cape flora, comments on the similarity of habit shown, in the conditions of that region, by plants genetically widely separated, and continues: "The second class . . . consists of plants which suddenly spring up and flower for a very short time after a shower of rain. They are almost all bulbous or tuberous and many Orders have developed bulbs which usually show no trace of them. For example, the whole section *Hoarea* of the genus *Pelargonium* is bulbous. . . ."

Corm and Bulb Formation in many Lines of Descent.

The appearance of the same character in different forms of life and different lines of descent has been fully discussed by Arber (4) in the chapter "Parallelism in Evolution." Vavilov (37) states that linneons and genera, more or less related to each other, are characterized by a similar series of variation with such a regularity that, knowing a succession of varieties in one genus or linneon, one can forecast the existence of similar forms and even similar genotypical differences in other genera and linneons. The similarity is the more complete as the linneons and genera are more nearly allied. Vavilov points out, however, that there is parallel variation even in families not closely related, and that, in general, parallelism is noticeable in organs having the same form and function.

The appearance of corms and bulbs is then a possibility in many lines of descent particularly (1) if a line has not already evolved too far in some other direction, (2) if the environment is such as to make this obviously adaptive character one that would be selected for its survival value. As regards (1) Huxley is illuminating. He remarks (22): "In any case we must beware of arguing that the inability of specialized forms to produce new types must be due to an inherent lack of genetic variability. This assertion is often made but cannot be upheld. We have already seen that the failure lies in the difficulty for selection of utilizing any variations except

those tending towards a further specialization in the same direction. When the biomechanical limit has been reached, the type is stuck and can do nothing but either maintain itself or else become extinct. However, as we have seen, such limits are relative to the environmental situation. If this is radically altered, evolutionary radiation may again set in, showing that the previous standstill was not due to lack of genetic variability."

As an example of such renewed evolutionary radiation the present writer would cite the bulbous *Droseras* of West and South Australia. As an example of a type which usually specializes in one direction but had not gone too far in that direction to be unable to switch over to another, he would mention the case of *Euphorbia tuberosa*. While many of the *Euphorbias* of the Old World, which grow in arid regions, have developed succulence and spines, this species, without stem-succulence or spines and with only slightly fleshy leaves, has developed a subterranean tuber about 5 cm. in diameter.

The tendency to form such organs is certainly deep-set among the potentialities of the *Phanerogams*.

It is, of course, possible that there may be a common ancestor for certain small groups within one geographical area, such as the *Melicas* of the western States of America or the bulbous *Droseras* of Australia, but at the moment there is no conclusive evidence for such a belief.

Factors affecting Tuberization.

Buchenau (10) records some interesting observations on the relative parts played by genetic composition and environment in the production of corms and bulbs in the *Juncaceae*. He considers that *Luzula nodosa* normally has tuberous thickenings, while in certain species of *Juncus* the appearance of these thickenings is very much influenced by climatic conditions. Attacks of certain fungi and insect larvae also induce tuberization. Jefferies (23) reports similar effects by the attack of the gall-midge on *Molinia caerulea*, where the attack prevents the development as a storage organ of the basal node and causes the food reserve to be deposited in the leaf sheaths around the nest of larvae and in the subjacent cord roots. Arber (4) discusses the influence of a fungus in causing tuberization in the *Ophrydeae* and quotes work by Bernard indicating that the influence of the fungus may be imitated by the action of certain sugars.

Vochting (38), following up much earlier and almost forgotten work by Knight, found that, by sufficiently varying light, tempera-

ture and moisture along with some manipulation of the plant parts, it was possible to induce tuber formation in any part of the potato plant.

Tincker (34, 35, 36) showed that shortening the daily period of light to ten hours decreased growth and increased tuberization in *Helianthus tuberosus* and in artichoke.

This influence is exerted through the translocation and utilization of the photosynthetic compounds. In the fourteen hours of darkness the treated plants have a longer time free from the manufacture of carbohydrates in which to remove the carbohydrates from leaf and stem to tuber. It is worth noting, in this connection, that the majority of the bulb- and corm-forming grass species occur in the zones (1) between the Tropic of Cancer and latitude 45° N. and (2) between the Tropic of Capricorn and 45° S. These are, of course, the zones within which most of the regions of Mediterranean climate lie, and that climate may be the most important factor in the selection of corm- and bulb-forming plants for survival, but it is permissible to speculate that the tuberizing tendency, when originated and selected, may be enhanced by a medium day-length.

Doposcheg-Uhlar (12) studied the formation of foliage shoots and tubers in water-culture on stems of the Gesneraceae. He came to the conclusion that the concentration of the nutrient had no effect on the final destiny (foliage shoot or tuber) of any particular bud.

The present writer experimented in the continuous removal of the inflorescences of both types (with and without corms) of *Arrhena-therum avenaceum*. There was no appreciable difference in corm formation in the one type and no stimulation to any kind of basal swelling in the other.

SUMMARY AND CONCLUSIONS.

1. The corm- and bulb-forming species of the Gramineae are listed and some details given regarding their individual peculiarities.

2. Their geographical distribution is discussed. Most of them are found where a Mediterranean climate exists. Some occur in steppe or semi-desert and a few are swamp plants. Several are found at high altitudes.

3. Corms and bulbs in the Gramineae are devices for tiding over the hot dry season of the Mediterranean climate and for giving a flying start when the growing season recommences. There are a few cases in the Gramineae and several outside that Order where a cold season is escaped by the same means.

4. Reference is made to the occurrence of corms and bulbs in many unrelated Orders throughout the Phanerogams. It would appear that the potentiality of forming these structures is widespread, that mutations giving such structures have frequently occurred in various lines of descent, and that selection due to environment has then made itself felt.

5. The expression of the character (corm or bulb formation) is, in many species, uneven. There is often a range of forms showing all grades from absence of such structures, through intermediate stages to marked development of corms and bulbs. This is doubtless due to the interaction of varying genetic composition and varying environment.

6. The immediate internal stimuli to corm or bulb formation are at present obscure. The effects of insect or fungus attack, which may be simulated by the application of certain sugars, would seem to give some pointers. Length of day has an undoubted influence on tuberization. The facts that drought stops growth even more than it stops photosynthesis and that, in some circumstances, there is an increase of photosynthesis after the partial dehydration of the leaf may have some bearing on the storage of rapidly accumulating carbohydrates at the onset of the dry season.

ACKNOWLEDGMENTS.

The writer desires to express his great indebtedness to Sir William Wright Smith, F.R.S., Regius Keeper of the Royal Botanic Garden, Edinburgh, for permission to work in the laboratories of the Garden and to use its extensive Herbarium and Library; to Dr. Alexander Nelson, Ph.D., Lecturer in Plant Physiology, Royal Botanic Garden, Edinburgh, for the many facilities so cordially offered, for his interest in this work, for his unfailing help and advice and his keen and kindly criticism; to the Director of the Royal Botanic Garden, Kew, for herbarium specimens kindly sent on loan, and to Mr. C. E. Hubbard, F.L.S., Botanist at the Kew Herbarium, for help and advice; to the Directors of the Bureaux of Plant Genetics and of Pasture and Forage Crops for references and translations, to Miss E. Brueckner, Botanical Station, Kimberley, S. Africa, for seeds and specimens, and to Miss B. D. Inglis for her admirable drawings.

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AN ACCOUNT OF $\times$ POTAMOGETON SUECICUS RICHT. IN YORKSHIRE
AND THE TWEED. By J. E. DANDY and G. TAYLOR. (With
Plates IV–VIII.)

(Read 13th June 1946.)

The pondweed which forms the subject of this paper first aroused special interest in 1940. In June of that year, while collecting in the River Wharfe at Harewood, west Yorkshire, we took specimens of what appeared to be the familiar *Potamogeton pectinatus* L., a species recorded from the Wharfe in F. A. Lees's "The Flora of West Yorkshire" (1888), p. 418.* When, however, the material, which was without flower or fruit, was examined after drying, it was noticed to have remarkably blunt leaves for *P. pectinatus*, and, this circumstance having led us to dissect the leaf-sheaths, these were found to be tubular towards the base, a character definitely excluding the plant from *P. pectinatus* which has open convolute sheaths. Now the two characters mentioned—blunt leaves and tubular sheaths—are found in *P. filiformis* Pers. and are in fact used to distinguish that species from *P. pectinatus* in the absence of fruits; but *P. filiformis*, apart from fossil remains, is not known from England, its only authenticated British station south of the Scottish border being in Anglesey.† The occurrence of this boreal species in a much-frequented and well-explored part of Yorkshire was so little to be expected that we decided to study the characters and distribution of our plant much more thoroughly before venturing to identify it. Now, after carrying out extensive surveys of the Wharfe and neighbouring rivers, and after collecting and examining some hundreds of specimens, we need no longer delay publication of our findings. If our identification of the plant is correct, this pondweed is of outstanding interest to students of British plant-distribution and we therefore give a considerable account of it.

* Lees recorded the species both as *P. pectinatus* L. ("In the Wharfe from Ilkley") and as *P. flabellatus* Bab. ("Bolton Bridge to Newton Kyme"). Numerous authors in addition to Lees have maintained *P. flabellatus* as a distinct species, but we are unable to do so. It is to be noted that Hagström (Crit. Res. Potamog., 48 (1916)) placed *P. flabellatus* under *P. pectinatus* forma *interruptus* (Kit.) Hagstr., and it is fair to comment that, in general, Hagström's formas represent mere habitat states or developmental phases.

† Records of *P. filiformis* as a recent plant have at times been published from various English localities, but none is credited. Thus Lees (*loc. cit.*) excluded one from the Barnsley Canal in South-west York. There is little doubt that these records were based on slender-leaved states of *P. pectinatus*.

IDENTIFICATION.

In August 1940 we obtained abundant material, including flowering specimens, from the locality in the River Wharfe at Harewood where we had first seen the plant, and shortly afterwards we found it at Leathley, higher up the same river. Also in 1940 we collected what proved to be the same plant in the River Ure at West Tanfield, Norton Conyers, Nunwick, Littlethorpe and Langthorpe, the material from West Tanfield being in flower (Plate VI).

Subsequently, in the years 1941–45, besides re-collecting the plant at some of the localities already mentioned, we gathered it in the Wharfe at Arthington (Plate VII), Weeton, Netherby, Ulleskelf and Ossendyke, and in the Ure at Masham and Ripon as well as in a tributary of that river at Westwick (Plate VIII). A good proportion of these specimens was in flower.

Furthermore, we found that our long series of specimens was supplemented by some old gatherings of the same plant made in the Wharfe at Pool by F. A. Lees (1868), at Linton by the same collector (1880), at Arthington by J. Abbott (undated), and at Wetherby by J. Jackson (1881); also in the Ure at Sharow by G. Nicholson (1880) and near Ripon by H. H. Slater (1881). All these had been named as *P. flabellatus*, and as we have seen no other specimens named *P. flabellatus* from the Wharfe or the Ure there can be no doubt that our plant is the one recorded from those rivers under that name in Lees's "Flora", to which reference has already been made.

The reader will remember from our opening paragraph that the first sample of the plant obtained at Harewood had remarkably blunt leaves and leaf-sheaths which were tubular towards the base—characters excluding it from *P. pectinatus* and suggesting *P. filiformis*. Study of the material which subsequently became available showed, however, that the plant is by no means constant in these characters. The leaf-apex varies considerably, though it tends to be more obtuse than in *P. pectinatus*. The sheaths vary too: some of them are obviously tubular towards the base as in the first specimens examined, but others are tubular only at the very base and many appear, at least by ordinary methods of dissection, to be quite open.* Certainly the variation shown is too wide for *P. filiformis*, in which species the leaf-apex is never acute and the sheaths are always manifestly tubular for some distance above the base.

* Miss Bance (see below), using the microtome and the anatomist's more exact technique, finds the sheaths always tubular at least at the very base in the material examined by her.

In view of this instability in vegetative characters an examination of the flowering material promised interesting results. When flower-spikes were first collected it was observed that in the young state they were congested and looked normal, but that on elongation they became much interrupted and had the appearance of being barren. That they are in fact abortive now seems certain, for never, despite repeated search, have we been able to find the plant in fruit or even showing signs of developing fruit; and though *Potamogeton* spikes frequently fail to produce fruit when growing in running water their genuine barrenness in the present case is confirmed by an examination of the pollen, which shows that the adult grains are mostly misshapen and in all probability impotent. Thus the flowers display a most interesting and significant character: that of apparently complete sterility.

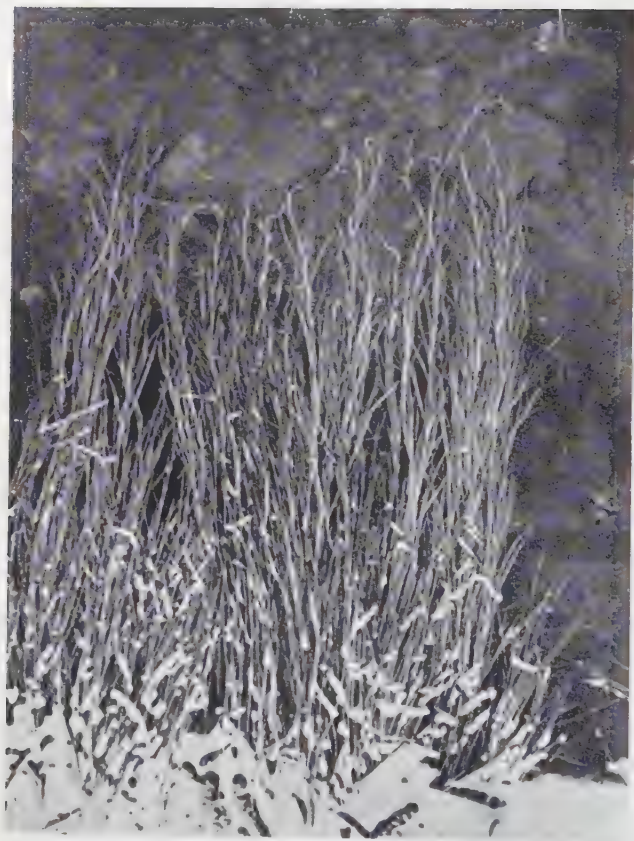
The characters used for separating *P. filiformis* from *P. pectinatus* include not only the form of the leaf-apex and the structure of the sheaths but also the shape and size of the fruits and the form of the carpels which produce them. Fruits, as already pointed out, are unknown in our plant; but an examination of its carpels proved revealing. These, unlike the leaf-apex and sheaths, are remarkably constant in form in the various gatherings investigated, and they resemble the carpels of *P. filiformis* in having broad sessile stigmas which lack the stylar "neck" characteristic of *P. pectinatus*.

To sum up, then, we have a plant which, on account of its sessile stigmas and (at least frequently) tubular sheaths, cannot be referred to *P. pectinatus* though it closely resembles that species in habit and general appearance; and which, on the other hand, cannot be referred to *P. filiformis* because of the instability in sheath-structure and leaf-apex. Its characters, moreover, present none sufficiently distinctive to suggest a third species; indeed in every way they combine the characters of *P. filiformis* and *P. pectinatus* and include nothing, apparently, which is not found in one or both of those species. These facts, reinforced by the evident abortiveness of the flowers, have led us to the conclusion, surprising though it may be, that the plant is a hybrid between *P. filiformis* and *P. pectinatus* and is therefore referable to $\times P. suecicus$ Richt.* The surprise, of

* This identification, arrived at by ordinary taxonomic methods, is confirmed by the anatomical researches of Miss H. Margaret Bance, who at our suggestion undertook a comparative study of *P. filiformis* and *P. pectinatus* in relation to the plant in question. Miss Bance's results are published elsewhere in this volume, but we should like to take this opportunity of expressing our appreciation of her painstaking work.



Potamogeton succicus. A typical bed of the hybrid in the River Ure at West Tanfield, north-west Yorkshire. Photographed 6th August 1945.



× *Potamogeton suecicus*. A close-up view of part of the bed shown in Plate IV. The elongated shoots, some of them with flower-spikes, are seen streaming in the current, in shallow water over a gravelly substratum. Photographed 16th August 1945.



× *Potamogeton sueticus*. Flowering specimens from the River Ure at West Tanfield, north-west Yorkshire. Collected 29th August 1940.



× *Potamogeton suecicus*. Flowering specimens from the River Wharfe at Arthington, mid-west Yorkshire. Collected 19th July 1945.

course, lies in the fact that the plant occurs well outside the accepted present range of *P. filiformis*.

DISTRIBUTION IN YORKSHIRE.

In giving an account of the distribution of × *P. suecicus* in Yorkshire we of course cannot claim to have carried out a complete survey of the relevant area, but the River Wharfe has been explored fairly thoroughly from Bolton Abbey to its confluence with the River Ouse; the River Nidd has been examined at many places from Lofthouse to Cattal; the River Ure and its basin have been visited at various points from Semer Water to the junction with the River Swale. The Swale (as far up as Downholme), the Ouse (as far down as Selby), and other rivers of the Ouse system such as the Wiske, Aire and Derwent have been examined at numerous places.

It is convenient first to deal with the parent species of × *P. suecicus*. *P. filiformis*, though carefully looked for, has not been found in any Yorkshire river; indeed this species has never been found in England apart from fossil remains. *P. pectinatus*, on the other hand, occurs quite frequently in the Ouse, Swale, Derwent and some other rivers of the Ouse system, as well as in canals and other waters in the same area; but we have been unable to detect this species in the Nidd,* while in the Ure we have found it only at one point in the lower portion at Littlethorpe, and in the Wharfe only in the lowermost reaches near the junction with the Ouse. It is a noteworthy fact that we have been unable to find any representative of *Potamogeton* subgen. *Coleogeton* † in the Nidd, and that most stretches of this river, particularly in its upper parts, are peculiarly deficient in aquatic vegetation where physical conditions, at least, appear very similar to those of the prolific and not far distant waters of the Ure and Wharfe; indeed the Nidd shares with those rivers a high reputation for trout-fishing qualities.

Turning to × *P. suecicus*, we find that this hybrid is apparently restricted in Yorkshire to the rivers Ure and Wharfe, and a notable

* Lees, Fl. W. York., 418 (1888), recorded *P. flabellatus* in the Nidd from "Ripley to Cowthorpe", but we have never seen a specimen.

† This subgenus includes *P. pectinatus*, *P. filiformis* and allied species. It differs fundamentally from the rest of the genus in having hydrophilous instead of anemophilous pollination. The only other European species, apart from *P. pectinatus* and *P. filiformis*, is the circumpolar *P. vaginatus* Turcz., which does not reach the British Isles though it has been falsely reported from Zetland. *P. vaginatus*, like *P. pectinatus*, has open convolute leaf-sheaths and so was excluded from consideration in the identification of the Yorkshire plant.

point about this, apart from the absence of *P. filiformis*, is that these two rivers appear to be remarkably deficient in *P. pectinatus* also. Thus in Yorkshire, as far as our evidence goes, $\times$ *P. suecicus* occurs in complete isolation from one of its parents and only rarely in association with the other. It was expected that the hybrid would occur in the main river (Ouse) below the points of entry of the Ure and Wharfe; but we have been unable to detect it in the places visited.

In the Ure the highest point at which $\times$ *P. suecicus* has been collected is at Masham, the lowest at Langthorpe, two or three miles above the confluence with the Swale. The highest point at which the hybrid has been observed in the Wharfe is at Leathley, the lowest at Ossendyke, three or four miles above the junction with the Ouse. Both in the Ure and in the Wharfe the plant grows in great profusion, usually forming massive colonies wherever it occurs (see Plate IV), sometimes in company with *P. perfoliatus* L. or with the unrelated *Ranunculus fluitans* Lam. and *Myriophyllum alterniflorum* DC. In the higher reaches it thrives on a gravelly substratum in a powerful current (see Plate V), but it favours also the deep weir-pools, while in the lower and more sluggish stretches, on the thick slimy silt, it forms huge beds with elongated shoots up to several feet in length streaming in the current. It was found flowering in a torrential mill-race in the Ure at West Tanfield. At Westwick, in a tributary joining the Ure from the south, the hybrid almost chokes the stream, and into this locality, where the current is slight, the plant has evidently been carried from the Ure in time of flood.

DISTRIBUTION IN THE TWEED.

In 1942 a plant identical with the Yorkshire $\times$ *P. suecicus* was discovered in the lowermost reaches of the River Tweed near Union Bridge, growing in situations similar to those which it frequents in the rivers Ure and Wharfe. The Tweed has been examined at many places from its source to the sea but the hybrid has been observed only a few miles above the tidal estuary. *P. pectinatus* was found growing in close proximity, but *P. filiformis* has not been detected in the Tweed although it occurs in Coldingham Loch, in north-east Berwickshire, eleven miles to the north of Union Bridge.

HABIT AND MEANS OF PROPAGATION.

As found in the rivers Wharfe, Ure and Tweed $\times$ *P. suecicus* is a conspicuous plant throughout the year and appears always to be

in an active state of growth. The thickish, copiously branched rhizomes, which are commonly white with reddish-brown speckling, penetrate the substratum at various depths, somewhat shallowly when growing in gravel but down to at least a foot in fine silt. In time of flood quantities of the plant are to be seen uprooted and drifting in the eddies or into the quiet backwaters, and pieces so carried have been observed to root and establish themselves in their new situation. This was one of the reasons why we expected the plant to occur in the main River Ouse below the points of entry of the Ure and the Wharfe; but, as we have already stated, it has not been found there.

Another and less accidental mode of increase and dispersal is by the formation of a succession of winter-buds or turions on the leafy shoots towards the end of the flowering season. The period of flowering is unusually prolonged, despite the sterility of the flowers, and flower-spikes in the early stages of development have been noted from the beginning of June to the beginning of November. Commonly the flowering shoots branch freely beyond the inflorescence and bear turions on the branches so formed.

The flowers, as already explained, appear to be entirely abortive, no fruit being formed, so that the plant depends for its propagation on the vegetative means just described. It is indeed possible, under one interpretation of the hybrid's origin, that all the individuals in Yorkshire and the Tweed belong to a single clone; but this is a point to be discussed further on.

In the water × *P. suecicus*, in its various phases, resembles the corresponding riverain states of *P. pectinatus* and is sometimes distinguishable from them only with difficulty. If flower-spikes are present the hybrid can at once be recognized by the form of the carpels with their *filiformis*-like stigmas. Again, the occurrence of tubular leaf-sheaths is a sure sign of the hybrid; but, as with *P. pusillus* L. and its allies, the structure of the sheaths is not readily ascertainable in fresh specimens and can only be satisfactorily determined by careful examination of properly prepared material under the microscope. Whether or not the sheaths are obviously tubular, however, they incline to remain enfolding the stem, and this, coupled with the form of the leaf-apexes (which, though variable, have a marked tendency to be obtuse or even rounded), will best serve to distinguish the hybrid from *P. pectinatus* when the more definite characters are not discernible.

Average samples of × *P. suecicus* from the Yorkshire rivers and the Tweed are more luxuriant and robust than average specimens

of the hybrid which we have seen from north and west Scotland, but these latter, it must be pointed out, were not from deep swift rivers. The riverain plant more closely resembles specimens from rivers of Jutland, in Denmark.* Its vigour is doubtless due to conditions of habitat.

AN ANOMALOUS DISTRIBUTION AND ITS POSSIBLE CAUSES.

The occurrence of $\times P. suecicus$ in Yorkshire and the River Tweed, apparently quite outside the present range of one parent species and only occasionally in association with the other, presents a distributional anomaly of which the possible explanations are well worth consideration. (See fig. 1.)

P. filiformis, one of the parents, is a boreal species in the British Isles, where it has been found growing only in Scotland (as far south as Berwickshire, Midlothian and Ayrshire), in north-western Ireland and in Anglesey, this island affording a very interesting outlying station.† The other parent, *P. pectinatus*, has an almost world-wide distribution and is in fact the most widespread of all *Potamogeton* species; its range in Britain extends from the south coast northwards to Zetland and the Hebrides, and it is found in most parts of Ireland as well as in the Isle of Man. Both are lowland species, rare in mountainous districts but frequent near the sea and not averse to brackish water. Their co-existence in Britain becomes more and more sporadic as we proceed southwards from Zetland and the Hebrides until it ceases altogether (apart from the outlying station in Anglesey) in the south of Scotland. Wherever they occur in close proximity the hybrid $\times P. suecicus$ is to be looked for, and its known stations in the north and west of Scotland are all within the joint range of the parent species.

The limited area of Yorkshire in which $\times P. suecicus$ occurs lies approximately 120 miles south of the nearest Scottish station (Coldingham Loch, in Berwickshire) known for *P. filiformis*; and its distance from the outlying station of that species in Anglesey is roughly the same. On the other hand the section of the Tweed in

* The Danish plant was correctly referred to $\times P. suecicus$ by Hagström (Crit. Res. Potamog., 23 (1916)), but he confused the issue by placing it under forma *Kernerii* Hagstr. which is based on a plant from the Tyrol. In our opinion this Austrian plant is not a hybrid but a state of *P. filiformis*; see Journ. of Bot., lxxviii, 147 (1940).

† There is fossil evidence that during the later glacial period *P. filiformis* occurred as far south as the Lea Valley in Middlesex. The species was recorded by Reid and Chandler (in Quart. Journ. Geol. Soc. London, lxxix, 605 (1923)) in a list of the Barrowell Green (Lea Valley) arctic flora.



× *Potamogeton suecicus*. Flowering specimens and broad-leaved sterile shoots from a tributary of the River Ure at Westwick, mid-west Yorkshire. Collected 26th September 1943.

which × *P. suecicus* has been found is only eleven miles south of Coldingham Loch, though still without the range of *P. filiformis*.

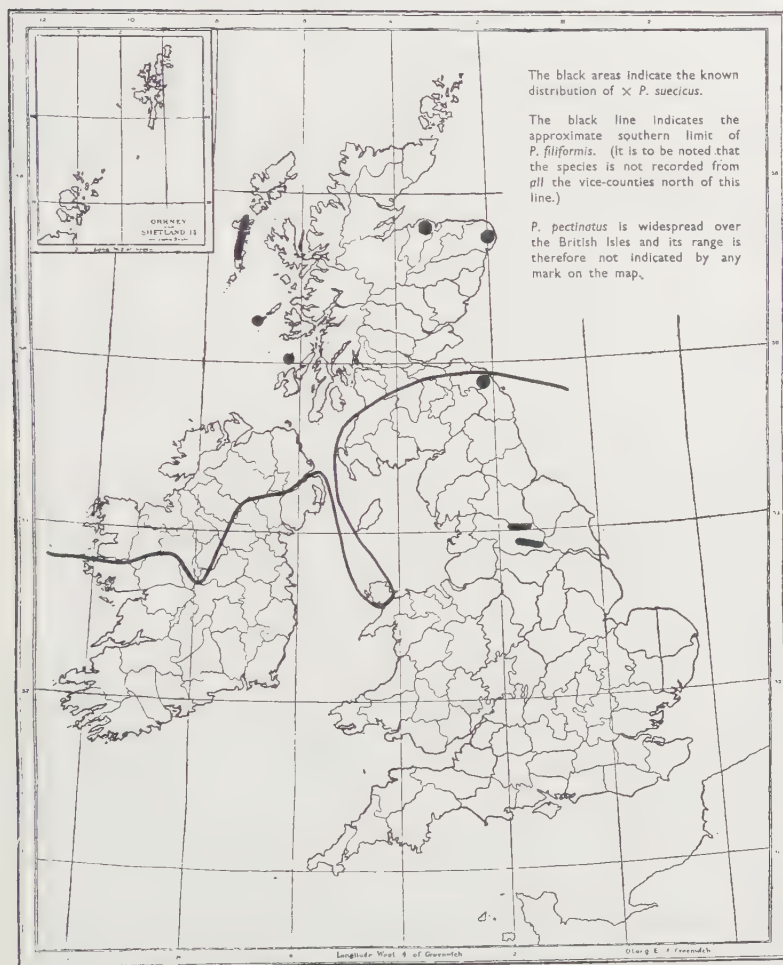


FIG. 1.—Map showing the distributions of × *Potamogeton suecicus* and *P. filiformis* in the British Isles.

P. pectinatus, as we have already stated, is found in the same part of the Tweed as × *P. suecicus*, but in the Yorkshire rivers, so far as our investigations have been able to discover, this association of hybrid and parent occurs only in a short section of the Wharfe not far above its junction with the Ouse, and at one point in the lower Ure at Littlethorpe. Higher up the Wharfe, as elsewhere in the

Ure,* we have been unable to detect the presence of *P. pectinatus* though this species grows quite frequently in the Ouse, the Swale and some other rivers of the Ouse system.

Taken by itself, the occurrence of $\times$ *P. suecicus* in the lower reaches of the Tweed, in association with *P. pectinatus* and only a few miles away from the nearest known station of *P. filiformis*, would not, perhaps, be a cause for great astonishment or speculation. But how are we to account for the presence in abundance of the same hybrid in two Yorkshire rivers which are widely removed from the present-day area of *P. filiformis* and which, moreover, appear to lack *P. pectinatus* except at a few points in the lower reaches? It is remarkable that $\times$ *P. suecicus* has not been found in the Ouse (into which the Ure and the Wharfe both flow) or in the Nidd (which lies between them); but even if the plant were to be discovered in these rivers, or (as may well happen) in any of the river-systems which lie between Yorkshire and the Tweed, the anomaly in its distribution would remain.

It is not possible for us to say whether *P. filiformis* and *P. pectinatus* have been associated in Yorkshire and the Tweed in recent, that is to say post-glacial, times. If we knew that such an association had occurred we should of course presume that $\times$ *P. suecicus* had originated recently and *in situ* in the rivers concerned. There is, however, no evidence at all of the recent occurrence of *P. filiformis* in northern England; and if the hybrid had originated in the Yorkshire-Tweed area during the post-glacial period it would be reasonable to expect that *both* parent species would have survived in this region, where climatic conditions have, it is generally believed, altered little in the time. We therefore think it not too fantastic to suggest that, in the area concerned, $\times$ *P. suecicus* may be a relic of a former vegetational epoch and that its occurrence there may date from per-glacial or inter-glacial times, the plant surviving any later glaciations. Its present strange localization has every appearance of having been determined solely by geological events, and no peculiar ecological conditions can explain its persistence in the Wharfe, Ure and Tweed. Such a view corresponds with that expressed by Wilmott (in Proc. R. Soc. London, Ser. B, cxviii, 221 (1935)) in discussing the Teesdale assemblage of local species.

If, however, in our exploration of the possibilities, we make this

* It should be remarked that Lees, in *The Naturalist*, x, 138 (1885), recorded *P. pectinatus* from Semer Water, at the head of the Ure. He did not repeat the record in his "Flora of West Yorkshire" (1888), however, and we have not seen any vouching specimen. Two visits to the lake in recent years have failed to produce confirmation of the record.

assumption that the occurrence of × *P. suecicus* in Yorkshire and the Tweed dates from per-glacial or inter-glacial times, are we to assume also that the plant originated *in situ*, that is to say by hybridization of *P. filiformis* and *P. pectinatus* within the area concerned? This second assumption would require that the two parent species were brought into close association within the area at some stage during the forced migrations of the glacial periods, and interbred before the (now) boreal *P. filiformis* was forced to retreat to its present limits. It would also require that *P. pectinatus* has since largely vanished from the Ure and Wharfe, having, perhaps, been ousted by the more vigorous growth of the hybrid. Further, under this assumption there would be no ground for supposing that the individuals of × *P. suecicus* in the two Yorkshire rivers and the Tweed belong to a single clone; on the contrary, it would be necessary to expect that the hybrid had had at least two or three independent points of origin within the region.

We have no evidence to help in deciding the points just raised, whether *P. filiformis* and *P. pectinatus* ever grew together in Yorkshire and the Tweed during the glacial periods, whether × *P. suecicus* throughout the region represents a single clone, and whether *P. pectinatus* was formerly more widely distributed in the Wharfe and the Ure than it is to-day. There is, however, another possible explanation of the hybrid's presence in the region which seems worthy of being put forward as it does not require the co-existence there at any period of the parent species, nor require more than one point of origin for the hybrid. It is that × *P. suecicus* in Yorkshire and the Tweed is itself a survivor of the flora displaced southwards by the advance of one of the ice-sheets. Under this theory the plant could represent a single clone of more northern origin and need at no stage of its migration have been in association either with *P. filiformis* * or with *P. pectinatus*; with or without the parent species it would have been forced south in the general displacement of the vegetational zones and have survived where it is now found on the retreat of the ice, though destroyed along its migrational paths. Such an explanation would perhaps best account for the facts of the hybrid's present distribution so far as we have been able to ascertain them; but as we have no evidence about the

* Clearly, in view of its boreal tendency, *P. filiformis* could not have escaped similar geographical disturbance though its migrational routes need not necessarily have coincided with those forced upon × *P. suecicus*; in fact its outlying station in Anglesey and its distributional trend in Ireland (*i.e.* to the north-west) suggest that it may have been compelled to follow a more westerly course.

capability for migration of a sterile aquatic hybrid of this type we are not prepared to support the theory to the exclusion of others. Indeed we know little about the overland migration of pondweeds, though it is certain that by some agency (birds are often suggested) the species are transported from one water to another, and in all probability vegetative disseminules (*e.g.* winter-buds) as well as fruiting-carpels are concerned.*

Whatever the truth, it is tempting to seek a connexion between the occurrence of $\times P. suecicus$ in Yorkshire and the sequence of events which led to the isolation in Teesdale of the remarkable assemblage of local species. The areas are only forty to fifty miles apart with a single low watershed separating the drainage systems concerned. In the copious literature dealing with the glacial geology of the region we have found no evidence either to confirm or controvert the views which we have expressed. The phytogeographical discussion in this account of $\times P. suecicus$ may, therefore, have some interest for those interested in possible results of glaciation in the area.

LITERATURE AND SPECIMENS, WITH VICE-COMITAL DISTRIBUTION.

Below we give a summary of the relevant literature, followed by a detailed list of specimens of $\times P. suecicus$ which we have seen from Yorkshire and the River Tweed, arranged under vice-counties. Four vice-counties are concerned, two in Yorkshire and two in the Tweed. Of the specimens cited, those collected by J. Abbott, F. A. Lees and H. H. Slater are in the herbaria of the Leeds City Museum, the Cartwright Memorial Hall (Bradford) and the Manchester Museum respectively, and this is indicated in the list; the other gatherings are all represented in the herbarium of the British Museum (Natural History).

P. FILIFORMIS $\times$ *PECTINATUS* =

$\times P. SUECICUS$ Richt., Pl. Eur., i, 15 (1890).—Hagstr., Crit. Res. Potamog., 20 (1916) excl. f. *Kernerii*.—Dandy & Taylor in Journ. of Bot., lxxviii, 145 (1940); *op. cit.*, lxxix, 101 (1941).—Clark & Harrison in Proc. Univ. Durham Phil. Soc., x, 220 (1940).—Harrison in Proc. Univ. Durham Phil. Soc., x, 263 (1941), 365 (1942).—Clark in Proc. Univ. Durham Phil. Soc., x, 373 (1943).

* The successful and rapid colonization of isolated inland waters by *Elodea canadensis* Michx., solely by vegetative means, indicates that sterility in aquatics need not be an impediment to overland migration.

P. flabellatus (non Bab.) F. A. Lees in Rep. Bot. Rec. Club, 1880, 150 (1882); Fl. W. York., 418 (1888) pro parte.—Slater in Bot. Trans. York. Naturalist. Un., i, 165 (1885).

Vice-county (64) MID-WEST YORK. R. Ure and neighbouring pool in meadow, Nunwick: 15th Sept. 1940, *G. Taylor*. R. Ure, Sharow: Sept. 1880, *G. Nicholson*. R. Ure, Ripon: Sept. 1881, *H. H. Slater* (herb. Manchester Mus.); 12th July 1942, *G. Taylor*. R. Ure, Littlethorpe: 12th Oct. 1940, *G. Taylor*. Tributary of R. Ure, Westwick: 27th June and 26th Sept. 1943, *G. Taylor*; 23rd July 1943, *E. C. Wallace*.

R. Wharfe, Leathley: 17th Aug. 1940, *G. Taylor*. R. Wharfe near Pool: July 1868, *F. A. Lees* (herb. Cartwright Mem. Hall). R. Wharfe, Arthington: without date, *J. Abbott* (herb. Leeds City Mus.); 19th July 1945, *G. Taylor*. R. Wharfe, Weeton: 10th Oct. 1943 and 29th Oct. 1944, *G. Taylor*. R. Wharfe, Harewood: 29th June and 2nd Aug. 1940, *G. Taylor*. R. Wharfe, Netherby: 12th Aug. 1945, *G. Taylor*. R. Wharfe, Linton, Collingham: 1880, *F. A. Lees* (herb. Cartwright Mem. Hall); 11th Aug. 1944, *G. Taylor*. R. Wharfe, Wetherby: Sept. 1881, *J. Jackson*; 11th Aug. 1944, *G. Taylor*. R. Wharfe, Ulleskelf: 2nd Aug. 1941, *G. Taylor*. R. Wharfe, Ossendyke: 25th June 1941, *G. Taylor*.

Vice-county (65) NORTH-WEST YORK. R. Ure, Masham: 6th Aug. 1945, *G. Taylor*. R. Ure, West Tanfield: 29th Aug. 1940 and 6th Aug. 1945, *G. Taylor*. R. Ure, Norton Conyers: 20th July 1940, *G. Taylor*. R. Ure, Langthorpe: 7th July and 29th Sept. 1940, 4th and 18th Aug. 1944, and 17th June 1945, *G. Taylor*.

Vice-county (68) CHEVIOTLAND. R. Tweed, Bankhead, Loanend: 30th Aug. 1942, *G. Taylor*.

Vice-county (81) BERWICK. R. Tweed above Union Bridge, Hutton: 30th Aug. 1942, *G. Taylor*.

The hybrid is already recorded for Vice-counties (93) NORTH ABERDEEN, (102) SOUTH EBUDES, (103) MID EBUDES and (110) HEBRIDES. Since this paper was read it has also been found in Vice-county (95) ELGIN: Innes Canal, Urquhart, 17th July 1946, *G. Taylor*.

We are indebted to the Director, Cartwright Memorial Hall, Bradford, for the loan of Lees's specimens; to Mr. J. Allen Baldwin, Harrogate, for the habitat photographs which form the basis of our Plates IV and V; and to Dr. Bernice G. Schubert of the Gray Herbarium, Mass., who kindly photographed the herbarium specimens shown in Plates VI-VIII.

A COMPARATIVE ACCOUNT OF THE STRUCTURE OF *POTAMOGETON*
FILIFORMIS PERS. AND *P. PECTINATUS* L. IN RELATION TO
THE IDENTITY OF A SUPPOSED HYBRID OF THESE SPECIES.
By H. MARGARET BANCE, B.Sc.

(Read 13th June 1946.)

In carrying out this investigation the aim has been to establish the identity of an interesting form of *Potamogeton* found commonly in the Rivers Wharfe and Ure in Yorkshire. Up to the present the plant has not been observed to produce fruits, the absence of which is suggestive of hybridity. Originally the plant was identified by Messrs J. E. Dandy and G. Taylor as $\times$ *P. suecicus* Richt., a hybrid between *P. filiformis* Pers. and *P. pectinatus* L., and they suggested that a detailed morphological examination of the supposed hybrid and of the suspected parents would test the validity of this identification.

The characters selected for the separation of species within the genus vary according to the different authorities. Hagström (2) regards the leaves, especially the submerged ones, to be of the greatest importance for distinguishing species. The shape of the apex, the form of the stipular sheaths both vary in the genus but are remarkably constant for the species. The internal anatomy of the stem is looked upon by Chrysler (1) as important; Hagström, while considering this, regards it as a criterion of lesser value than the leaf form. The internal anatomy of closely allied forms is very similar. However, the cells of the endodermis are of importance in this field since they show reasonable specific variation. The stelar structure also differs within the genus. The arrangement of the bundles varies according to the degree of vascular fusion that has taken place between the bundles.

It is therefore along these lines that the investigation has proceeded. The stem anatomy of the two species and of the supposed hybrid has been examined, also the form of the stipular sheaths, the leaf apices and the leaf margins. In addition to this the pollen and the carpels of the three plants have been examined in an endeavour to ascertain the cause of sterility exhibited in the supposed hybrid.

Potamogeton filiformis Pers. [Material examined: Cameron Reservoir, Fife, *K. N. G. MacLeay*, 25th June 1942 (in Herb. Brit. Mus.). Same locality, *H. M. Bance*, 28th May 1945 (in Herb. Brit. Mus.).]

(i) *Stem Anatomy at Internode.*

The stem is bounded by an epidermis which is lacking in stomata and composed of regular, squarish cells which are slightly cuticularized. Beneath this is a much enlarged cortex in which three regions are distinguishable. The outer cortex or hypodermis is a single layer of cells situated directly under the epidermis. The central region of the cortex is traversed by many large air channels. These are arranged in two circles and the lacunae towards the outside are larger than those towards the centre of the stem. At the intersections of the diaphragms separating the lacunae, cortical bundles are present. The number varies; at the base of the stem their number is greater than nearer the top. The cortical bundles are groups of a few fibres and are derived from the small bundles of the basal sheaths. The inner cortical region is made up of loosely packed parenchyma cells. The stele is centrally disposed. Externally it is bounded by an endodermis one cell thick. The cells are rectangular and thickened with lignin on their inner tangential and radial walls—hence described as U-shaped. In the central region of the stele there are four vascular bundles—two median ones and two lateral ones. Each one is composed of a xylem lacuna surrounded by phloem tissue. Between the bundles is packing parenchyma.

(ii) *Leaf* (fig. 1).

The leaves are vaginate, linear, with obtuse apex and entire margin. There are three nerves running the entire length of the leaf. The stipular sheath is closed and tubular. It is adnate to the leaf base and extends from the node for a distance varying from 9–14 mm.

Potamogeton pectinatus L. [Material examined: Cameron Reservoir, Fife, *H. M. Bance*, 30th October 1944 (in Herb. Brit. Mus.). Wilstone Reservoir, Tring, Herts, *J. E. Dandy* (1183), 24th June 1945 (in Herb. Brit. Mus.). River Derwent, Buttercrambe, North-east York, *G. Taylor*, 28th August 1945 (in Herb. Brit. Mus.).]

(i) *Stem Anatomy at Internode.*

The epidermal and cortical regions of the stem are similar to those of *P. filiformis*. There is a slight cuticularization of the

epidermis and no stomata. In the cortex from 1-6 circles of air lacunae are present—the larger towards the outside and the smaller towards the inside of the stem. Cortical bundles are again present in one or two circles, their number decreasing from the base of the stem to the apex. The endodermis is made up of a single layer of cells with U-shaped thickening. There may be four, three, or one bundle in the stele, arranged respectively as two median and two

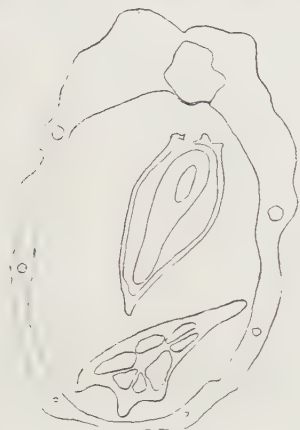


FIG. 1.—*P. filiformis*. T.S. stem at a short distance above node showing closed sheath. ($\times 120$)



FIG. 2.—*P. pectinatus*. T.S. stem at a short distance above node showing open sheath. ($\times 120$)

lateral bundles, one median and two lateral bundles, or simply one bundle.

(ii) *Leaf* (fig. 2).

The leaves are vaginate, linear, with entire margin and usually long acuminate apex. There are three or five nerves running the entire length of the leaf. The stipular sheath is open and convolute along its whole length which varies from 4-60 mm. in the different forms examined. It is adnate to the leaf base as in *P. filiformis*.

$\times$ **Potamogeton suecicus** Richt. [Material examined: River Wharfe, Weeton, Mid-west York, *G. Taylor*, 29th October 1944 (in Herb. Brit. Mus.). River Ure, Langthorpe, North-west York, *G. Taylor*, 18th August 1944 (in Herb. Brit. Mus.).]

(i) *Stem Anatomy at Internode*.

The anatomy of the stem is very similar to that of *P. filiformis*. The epidermis is a single layer of regular squarish lightly cuticularized cells. Three cortical regions are distinguishable, but in this

contents remain. A few cells of the intermediate layers are present.

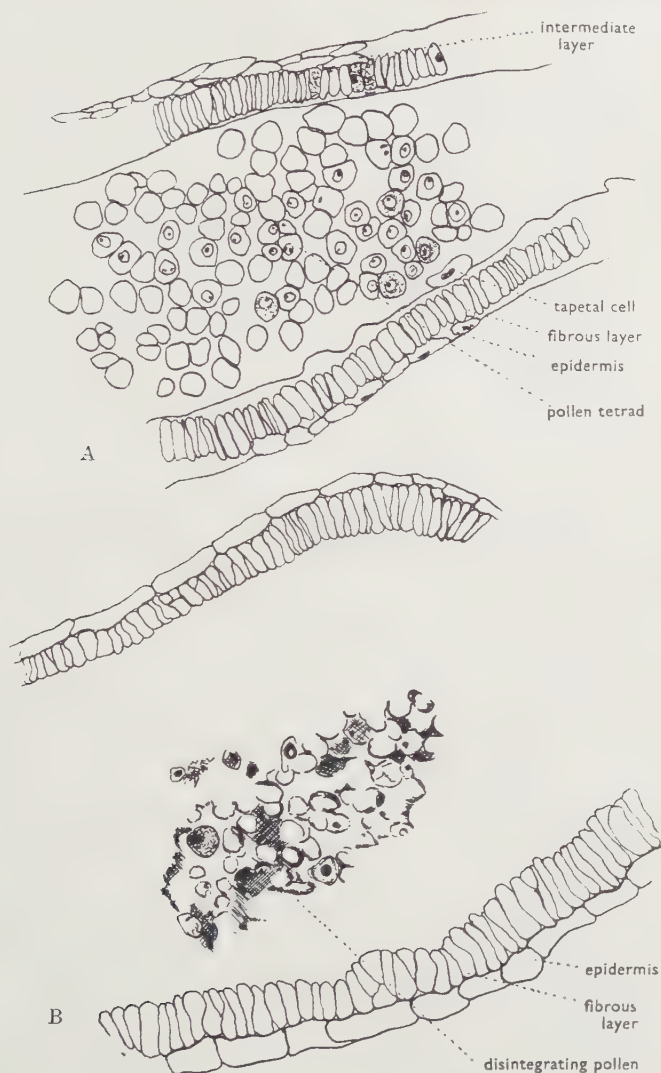


FIG. 4.—Anthers of *P. suecicus*.

- (A) Showing normal pollen, tapetal cells, fibrous layer and intermediate layer. ($\times 200$)
 (B) Showing disintegration of the pollen; anther wall composed of epidermis and fibrous layer. ($\times 200$)

For the most part the pollen grains still show their tetrad arrangement.

At a slightly later stage the tapetum and intermediate layers have disappeared with a corresponding increase in the development of the fibrous layer. In many of the cells the starchy contents have been absorbed. The pollen is perfectly normal and fills the pollen sac. There is a marked variation in the size of the grains however. In a few cases two nuclei, the normal number for the mature pollen grain, are visible, but generally there is only one.

At a later stage, when most of the cells of the fibrous layer are empty of starch, there is a noticeable reduction in the quantity of pollen in the sacs. The walls of the grains appear to have split and their contents seem to be in the process of disintegration. Completely empty pollen sacs are frequently found.

(b) *Carpels*.—In the material available, no stages in the development of the ovule could be traced. Development had proceeded as far as the formation of the embryo-sac. In this the fusion nucleus is visible together with three others, two at the chalazal end and one at the micropyle end. The normal eight nuclei of the embryo-sac lie embedded in the nucellus which is surrounded by a single integument. In no case has an embryo been found in the carpels examined.

DISCUSSION.

In spite of the fundamental similarity shown in the stem anatomy of the three plants (the form of the cortex, the presence of the cortical bundles, the U-shaped endodermis) the stele presents certain differences in which a developmental trend by reduction can be traced. The four-bundled arrangement of *P. filiformis* and $\times P. suecicus$ represents a stage not far removed from the normally three-bundled arrangement seen in *P. pectinatus*. The reduction in the number of bundles in *P. pectinatus* is brought about by the fusion of the two median xylem lacunae. Also in *P. pectinatus* can be seen the ultimate stage of reduction where one xylem lacuna only is present. This is brought about by the fusion of the median bundle and the two lateral ones. Therefore from the evidence of the stem anatomy alone, no conclusion can be reached with regard to the hybrid nature of the Yorkshire plant. The general similarity in the topography of the stem supports a close affinity between the species. The leaf provides further evidence to suggest a relationship between *P. filiformis*, *P. pectinatus* and the Yorkshire plant. The leaf apices of the putative parents differ to no small degree while the supposed hybrid is found with leaves whose apices are of both types. The leaf sheaths are of assistance in determining the relationship between

the three plants under discussion. In *P. filiformis* they are closed and tubular whereas in *P. pectinatus* they are open and convolute. The supposed hybrid shows an intermediate type. For a short distance above the node they are fused and then they become open and convolute. The intermediate form of the sheaths and the form of the leaf apices, showing both the *filiformis*-type and the *pectinatus*-type, suggest hybridity.

The sterility observed in the Yorkshire plant provided the first indication of its hybrid nature. Care is needed, however, in the diagnosis of any hybrid of *P. pectinatus* on this ground because that species itself under some conditions (*e.g.* in fast current) fails to develop fruit. In the supposed $\times$ *P. suecicus* the abortive nature of the pollen has been fully demonstrated and hence the reason for the failure to set fruit becomes obvious. Other reasons, in addition to the two above mentioned, which could also explain the lack of fruits, might be the deformation of the embryo-sac, but that is not the case in this instance, or a deformation of the embryo. However, in none of the material examined is there any sign of fertilization and hence of an embryo, which is probably due to lack of pollen in all plants.

As a result of these investigations the conclusion is reached that the plant from the Rivers Wharfe and Ure is in fact the hybrid $\times$ *P. suecicus* Richt.

The morphological observations may be conveniently tabulated as follows:—

	<i>P. filiformis</i>	<i>P. pectinatus</i>	$\times$ <i>P. suecicus</i>
Leaf apex .	obtuse	acute	obtuse to acute
Leaf sheath .	fused and tubular	open and convolute	intermediate
Endodermis .	U-shaped cells	U-shaped cells	U-shaped cells
Stele . . .	4 vascular bundles	4-1 vascular bundles	4 vascular bundles

The writer wishes to express her gratitude to the Staff of the Botany Department, St. Andrews University, for supervision of the work, and also to Dr. G. Taylor for his help and advice.

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PHLEUM ALPINUM L., EMEND. GAUD. AND *P. COMMUTATUM* GAUD.

By J. W. GREGOR. (With Plate IX.)

Linnaeus gave the name *Phleum alpinum* to the Mountain Timothy grass, but Gaudin (1808) pointed out that as far as Switzerland is concerned *P. alpinum* L. covered two different populations, the one a high alpine, the other an inhabitant of the less elevated situations: the former he called *P. commutatum*, retaining the Linnaean name *P. alpinum* for the latter. In 1835 Shuttleworth collected Mountain Timothy in Canton Valais, confirmed the presence of two distinctive races, and considered *P. commutatum* Gaud. as synonymous with *P. alpinum* of British authors but not with Linnaeus' species in its entirety (Shuttleworth, 1838). Babington (1843), appreciating the similarity between the high alpine plants and those found in Scotland, and regarding Shuttleworth's treatment as justified, recorded Scottish Mountain Timothy as *P. commutatum* Gaud. But the Scottish race still continues to appear in the British floras (the current 10th, 1922, edition of Babington's Manual not excepted) as *P. alpinum* L. The situation is further complicated, however, for Dickie (1860) mentions Braeriach and Cairntoul as habitats of *P. alpinum* L. var. *commutatum*, thus implying that both races occur in Scotland.

Cytologically the Scottish population proved to be tetraploid with twenty-eight somatic chromosomes (Gregor and Sansome, 1930). At the same time it was recorded that plants received from Sweden possessed the diploid number ($2n=14$), but in all probability these Swedish specimens were not indigenous material since the Swedish population, like the Scottish, is now known to be exclusively tetraploid. In her excellent cyto-genetic study of certain constituents of the genus *Phleum*, Nordenskiöld (1945) provides maps of the geographical distribution of both cytological types, and whereas the tetraploid form is seen to have a very extensive range including Central Europe, the diploid occurs only in Central Europe. In this common area the diploid is apparently more or less confined to the lower altitudes while the tetraploid is found at the higher elevations at or near the snow line.

Nordenskiöld's genecological classification (p. 127) is similar

to that proposed by Gregor (1931) who referred the two races of Mountain Timothy to separate ecospecies, and grouped them together with the diploid and hexaploid races of common Timothy (*P. pratense* $2n$ and $6n$) in the same coenospecies. Nordenskiöld, however, goes a step further and, in addition to recognising the genecological significance of diploid and tetraploid Mountain Timothy, proposes that they also be accorded taxonomic recognition at the species level. Thus she refers the tetraploid population to the taxonomic species *P. commutatum* Gaud. and the diploid to *P. alpinum* L. Gaud.

The cyto-genetic evidence has led Nordenskiöld to suggest that *P. commutatum* is an allopolyploid of unknown origin and to regard it as a somewhat isolated member of the coenospecies, for its two chromosome sets cannot be considered homologous, either with each other or with any other set in the coenospecies. Gregor and Sansome (1930) had previously suggested tentatively that this tetraploid Mountain Timothy occupied a key evolutionary position and was one of the ancestral forms of the cultivated hexaploid Timothy, having arisen as an amphidiploid by the doubling of the chromosomes in gametes of the hybrid between the diploid *pratense* ecospecies (now recognised taxonomically as *P. nodosum* L.) and the tetraploid mountain ecospecies, *P. commutatum* Gaud. However, the hexaploid amphidiploids obtained by Nordenskiöld by the fertilization of diploid gametes of *P. nodosum* L. with tetraploid female gametes of an octoploid race of *P. commutatum* are much less like the cultivated Timothy, though when crossed with the latter the likeness is increased. The inference, in all probability a correct one, is therefore, that the artificial hexaploids produced by Gregor and Sansome were not true amphidiploids but instead were natural crosses between unreduced female gametes of the triploid hybrids and normal male gametes of the hexaploid species.

Thus although the part played by the tetraploid Mountain Timothy in the evolutionary history of the coenospecies is apparently less spectacular than was at first imagined, its ecospecific status has been duly confirmed. Despite the close morphological resemblance between it and the diploid Mountain Timothy, the fact that these two ecospecies differ not only genetically and cytologically but also ecologically would seem fully to justify Nordenskiöld's proposal to accord them the rank of taxonomic species, in which case the Scottish Mountain Timothy would, as Babington suggested in 1843, belong to *P. commutatum* Gaud.

The following table summarizes the relationship between the

genecological units of both Gregor and Nordenskiöld and the taxonomic species recognised by the latter author.

GENECOLOGICAL UNITS		TAXONOMIC SPECIES
Gregor (1931)	Nordenskiöld (1945)	
COENOSPECIES	COENOSPECIES	
<i>P. pratense-alpinum</i>		
ECOSPECIES	ECOSPECIES	
<i>P. pratense</i> 2n	<i>P. nodosum</i> 2n = 14	<i>P. nodosum</i> L.
„ 6n	<i>P. pratense</i> 2n = 42	<i>P. pratense</i> L.
<i>P. alpinum</i> 2n	<i>P. alpinum</i> 2n = 14	<i>P. alpinum</i> L., Gaud.
„ 4n	<i>P. commutatum</i> 2n = 28	<i>P. commutatum</i> Gaud.

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FIG. 1.—Tetraploid Mountain Timothy collected at 3000 feet on Glas Maol, Scotland.



FIG. 2.—Diploid Mountain Timothy collected at 5500 feet on the Stripsenkopf, Austria.

Botanical Society of Edinburgh.

(FOUNDED 1836.)

Incorporating the CRYPTOGAMIC SOCIETY OF SCOTLAND.

OCTOBER 1946.



I.—NAME AND OBJECT.

1. The name of the Society shall be "THE BOTANICAL SOCIETY OF EDINBURGH".

2. The object of the Society shall be the advancement of Botanical Science, by means of periodical meetings, publications, correspondence, and such other means as the Council may from time to time determine.

II.—MEMBERSHIP AND RIGHT TO VOTE.

1. The Society shall be open to Ladies and Gentlemen, and shall consist of Ordinary Fellows, Lady Members, Ordinary Members, Honorary Fellows and Associates.

2. Only Honorary and Ordinary Fellows shall have the right to vote in connection with the business of the Society.

(a) ORDINARY FELLOWS.

1. A candidate for admission as an Ordinary Fellow must present an application signed by two Fellows. The application shall be read at the proper time during private business, and shall be submitted at the next Ordinary Meeting.

2. Ordinary Fellows shall, on admission, sign the Laws, and pay the sum of One Pound to the funds of the Society; and shall contribute One Pound annually thereafter at the October Meeting. Ordinary Fellows are entitled to receive the *Transactions*, provided their subscriptions are paid.

3. Ordinary Fellows may at any time compound for their annual contributions by payment of Fourteen Pounds, less an amount equal to one-third of the annual subscriptions previously paid.

4. The Council shall take such measures as shall be deemed advisable regarding Fellows whose subscriptions are in arrears.

(b) LADY MEMBERS.

Any Lady may, on the recommendation of the Council, be elected a Member for life on payment of a single contribution of Three Guineas. Lady Members shall not be entitled to receive the *Transactions*.

(c) ORDINARY MEMBERS.

The Society may elect Ordinary Members on the recommendation of the Council. The name of any candidate shall be submitted to the Council and, if approved, shall be submitted for election at the next Ordinary Meeting. Ordinary Members shall pay the sum of Five Shillings on admission, and shall contribute Five Shillings annually thereafter at the October Meeting. They shall not be entitled to receive the *Transactions*.

(d) HONORARY FELLOWS.

1. The Council shall be privileged to propose Ladies and Gentlemen for election as Honorary Fellows. The names of those proposed shall be stated in the Billet calling the Meeting at which they are to be submitted for election. Any Fellow may submit to the Council the name of any individual whom he wishes to propose.

2. The Honorary Fellows shall be limited to twelve British subjects and twenty-five subjects of Foreign countries.

3. Honorary Fellows shall be entitled to all the privileges of Ordinary Fellows, and shall receive copies of the *Transactions* free of charge.

(e) ASSOCIATES.

The Society shall have power to elect, on the recommendation of the Council, as an Associate anyone who has rendered special service to the Society by transmitting specimens or botanical communications. Associates shall receive copies of the *Transactions* free of charge.

(f) METHOD OF ELECTION.

The names of candidates submitted for election to the Society shall be read from the Chair, and the candidate shall be declared duly elected unless a ballot is demanded. Any such ballot shall be taken at the next Ordinary Meeting of the Society. The ballot shall be determined by at least two-thirds of the votes provided fifteen Fellows are present and vote.

(g) DISCIPLINE.

In the event of any Member acting in such a way as shall seem detrimental to the interests of the Society, the Council may recommend that the name of such Member be deleted from the roll. In the event of the Council taking this action, the recommendation shall be brought before the next Ordinary Meeting of the Society and voted upon by ballot at the immediately succeeding Meeting when, if the recommendation be adopted by a majority of two-thirds of the votes of at least fifteen Fellows, the name of such person shall be deleted from the roll of Membership.

III.—OFFICE-BEARERS.

1. The general direction of the affairs of the Society shall be in the hands of a Council, consisting of a President, four Vice-Presidents, ten Councillors, an Honorary Secretary, an Assistant Secretary, a Foreign Secretary, a Cryptogamic Secretary, and a

Treasurer, who shall be elected annually from among the Ordinary Fellows at the Ordinary Meeting in October. Five shall be a quorum.

2. The Council shall prepare a list of Fellows whom they propose to nominate as Office-Bearers for the ensuing year. This list shall be printed along with the Billet of the October Meeting. If a vote be demanded, Fellows shall vote by putting these lists into the ballot-box, with any alterations they may think proper to make. The lists shall not be signed. Every Fellow present at the Meeting is entitled to vote.

3. The Office-Bearers may be re-elected, except the two senior Vice-Presidents and the three senior Councillors, who shall not be eligible for re-election to the same offices till after an interval of one year.

4. The Council shall nominate annually an Auditor and an Artist, to be recommended to the Society.

5. The Treasurer shall receive and disburse all money belonging to the Society, collecting the money when due, and granting the necessary Receipts. His accounts shall be audited annually by the Auditor appointed by the Society. It shall be the duty of the Treasurer to place all money belonging to the Society in one of the Chartered Banks of this City, unless the same shall have been ordered by the Society to be otherwise invested; and he shall never keep more than Ten Pounds of the Funds of the Society in his hands at a time. The Bank Account shall be kept in the name of the Society, and all drafts thereon shall be signed by the Treasurer. The Treasurer shall submit annually a certified Statement of the Receipts and Expenditure of the past year, with the Auditor's Report thereon.

6. The Honorary Secretary, with the aid of the other Secretaries, shall give intimation of all General and Committee Meetings, shall Minute their proceedings in Books to be kept for the purpose, and shall conduct all the Society's Correspondence. He shall also take charge of all Donations of Plants and Books, and shall see them deposited in the Herbarium and Library, in conformity with any arrangements made by the Society with Government.

7. The Council shall have the power to fill any vacancy which may occur during the year.

Note.—Agreeably to an Act of the Town Council of the City of Edinburgh, dated January 8, 1839, the Professor of Botany in the University of Edinburgh is constituted Honorary Curator *ex officio*, with free access to the Society's Collection, whether a Member of the Society or not.

IV.—MEETINGS.

1. An Ordinary Meeting of the Society shall be held on the Second or Third Thursday of every month, from October to June inclusively.

2. Any Member may transmit to the Society Papers and Communications, which, if approved by the Council, may be read by the author, or, in his absence, by the President or Secretary, at any of the Ordinary Meetings.

3. Minutes shall be kept of the Meetings of the Society and of the Council, and the Minutes of each Meeting shall be read as the first business of the next ensuing Meeting of the same kind.

4. Each Fellow shall have the privilege of admitting a Visitor to the Ordinary Meetings of the Society at the close of the private business.

5. An Extraordinary Meeting of the Society may be called at any time, by authority of the Council, at the request of three or more Fellows.

6. The Council shall hold a Meeting for business before each Ordinary Meeting of the Society unless the President shall otherwise determine. The Council may at any time be called upon by the President, Vice-Presidents, or Secretaries to meet for the transaction of business.

V.—PUBLICATIONS.

1. The Society shall publish *Transactions* and *Proceedings*. The consideration of the acceptance, reading, and publication of all papers is vested in the Council, whose decision shall be final.

For the consideration of each paper the Council shall appoint two Referees, who shall submit their reports to the Council through the Honorary Secretary. Acceptance for reading shall not necessarily imply acceptance for publication.

2. The Council may from time to time fix special prices for the sale of copies of the *Transactions* to Fellows, Members, and Associates.

VI.—ALTERATION OF CONSTITUTION AND RULES.

Any motion for the alteration of the Constitution and Rules must be intimated to the Council, and shall be printed in the Billet calling the Meeting at which it is to be brought forward, and in the Billet of the Meeting at which it is to be considered. It shall then be determined by a majority of at least two-thirds of the votes provided at least fifteen Fellows are present and vote.

TRANSACTIONS
OF THE
BOTANICAL SOCIETY OF EDINBURGH

SESSION CX

PRESIDENTIAL ADDRESS: SOME REFLECTIONS ON INTRA-SPECIFIC
ECOLOGICAL VARIATION AND ITS CLASSIFICATION. By J. W.
GREGOR.

(Read 12th December 1946.)

The most important, and certainly the most practicable, ecological unit is the taxonomic species, but "if the actual relationships of organisms to their essential surroundings are to be interpreted correctly, the ecologist, the systematist, and the agriculturist must deal with the basic unit, the ecotype" (Lawrence, 1945, p. 313). The frequent references to ecotypes bear witness to the fact that ecotypic variation—hereditary, physiological and morphological differentiation of an adaptive kind—within the taxonomic species is by no means an uncommon phenomenon. Although the process of ecotype formation is fundamentally of greater biological interest than the end product, yet the ecotype has such a very real value as a reference category that for this reason, if for no other, it merits attention on its own account. Since the term ecotype is becoming increasingly popular with ecologists, bio-geographers and agriculturists, and since its significance as a variational unit depends very much on the way it is used, we shall take some examples from the literature on this subject and, with their aid, examine the nature of this most elusive variational category.

It was early appreciated that the ecotype concept had particular application to the improvement of cross-fertilising crop plants, and it is only natural that a considerable amount of the data relating to the ecotypic structure of species should have been obtained from forage plants. For instance, ecotypes have been recorded in such forage genera as *Agropyron*, *Agrostis*, *Arrhenatherum*, *Bouteloua*,

Bromus, *Dactylis*, *Festuca*, *Lolium*, *Medicago*, *Melilotus*, *Onobrychis*, *Phalaris*, *Phleum*, *Poa* and *Trifolium*. Nevertheless, the nature of the ecotype still remains something of an enigma. Turesson (1922) very wisely did not define his ecotype in more precise terms than "the product arising as a result of the genotypical response of an ecospecies to a particular habitat". It is evident, therefore, that before we proceed further the ecospecies needs some brief comment.

The term ecospecies, when first proposed by Turesson, was regarded by him as a superior ecological unit divisible into ecological sub-units—the ecotypes. Later the emphasis was shifted from ecology to inability freely to exchange genes with other populations in nature. This change, with its "in nature" stipulation, did little to establish the difference between the ecospecies and the ecotype, for not only was it virtually impossible from field observations to assess the status of distantly separated populations, but differentiation of any populations, ecotypes not excepted, implies the presence of some kind of barrier to the free flow of genes. The ecospecies is now a cyto-genetical unit without ecological implications, and ecotypes which are incapable of *freely* exchanging genes when given the opportunity of doing so under controlled experimental conditions, belong to different ecospecies—a point to remember when we come to discuss trends of ecotypic variation. We have, then, ecotypes which can exchange genes freely belonging to the same ecospecies, ecotypes between which gene exchange is restricted belonging to different ecospecies, and ecotypes which are incapable of exchanging genes belonging to different *coenospecies*. Such a classification of ecotypic variation, though often open to criticism, is obviously of primary importance to plant-breeders,* but it can hardly be expected to appeal to the practical taxonomist for the very good reason that partial, or even complete, genetic independence of groups of individuals is not necessarily associated with taxonomic, *i.e.*, morphological differences. In fact, Stebbins (1945 *a* and *b*), after reviewing the available evidence, suggests that there is no direct genetic connection between the causal agents of hybrid sterility and genes which produce the taxonomic differences. Clearly the criterion of morphological distinctness cannot be used for the separation of ecotypes of one more or less independent evolutionary series from those of another—a fact which should discourage attempts to establish the ecotype as a unit of the orthodox taxo-

* The recent taxonomic revision of *Gossypium* is a notable example of an essentially genecological classification of a genus which includes cultivated species. (HUTCHINSON, SILOW & STEPHENS (1947), Oxford Univ. Press.)

nomie system. An admirable discussion of the merits and demerits of the ecospecific concepts briefly outlined above can be found in Turrill (1946). However, the need for a new approach to classificatory problems is perhaps greatest at the lower variational levels, and, from the bio-geographic standpoint in particular, what is wanted is a classification which would adequately express the distributional continuities of population differentiation, physiological as well as morphological, within the species groupings. With this ultimate objective in mind we shall now return to the ecotype.

Ecotypes are formed, according to Turesson, by the predominant habitat factors selectively sorting out appropriate biotypes from a heterogeneous assemblage and welding them into specialised habitat populations. The ecotype as originally visualised is, therefore, quite obviously not a variate class; neither is the term restricted to the predominating type of variate in a habitat but covers all the habitat population constituents. It is quite definitely a population concept.

Turesson looks upon his ecotype as a relatively homogeneous population separated from neighbouring ecotypes of different heredity by a narrow zone of intergradation. Such an ecotype picture is readily appreciated, but it is the ecotype at its simplest, and from such favourable material it is unsafe to generalise. It is, however, undoubtedly true that where two strongly contrasting local habitats happen to adjoin one another, their respective populations often do possess just those features which Turesson describes.

Some further light is thrown on Turesson's conception when we examine his proposed classification of ecotypes. He recognises several kinds of ecotypes; for instance, his edaphic ecotypes are those which occupy situations where the selective effect of soil is predominant; in other localities he has delimited climatic ecotypes. This is apparent from the fact that his classificatory categories: *oecotypus alpinus*, *sub-alpinus*, *arenarius*, *campestris*, *salinus*, etc. cover both climatic and edaphic ecotypes. Thus only that part of a population's heredity which is found to be related to the most conspicuous habitat characters is used to determine the kind of ecotype, though the diagnostic characteristics are not limited to those features. On this basis, therefore, we can have in any one locality either a climatic or an edaphic or a biotic ecotype, but, as Sinskaja (1942) puts it, "two ecotypes of one and the same species cannot exist in the same habitat". On the other hand Kovalev (1939) recognises a sub-ecotype in the cherry plum, which suggests that he holds a different view. *Prunus caspica* Kov. et V. Ek., a

species with pubescent leaves and petioles and with plump, smooth or slightly pitted stones, grows along the western and southern shores of the Caspian Sea. Within this area there also occurs a cultivated race, *P. caspica* ssp. *foveata* Kov. et Streb., with compressed and finely pitted stones. Kovalev has called the species an ecotype and the sub-species a sub-ecotype. Although it is clear that Kovalev is not averse to sub-dividing the ecotype, it is by no means so clear whether this sub-ecotype does in fact occupy its own special ecological niche within the specific territory, or whether a mechanical separation of the two races is not maintained for cultural reasons. Indeed the impression one gets is that the classificatory division is essentially an orthodox taxonomic rather than a genecological one, an impression which, if anything, is strengthened when it is seen that of the eleven ecotypes listed everyone has been accorded either specific or sub-specific rank.

We have seen that Turesson considers ecotypes to be recognisably discontinuous variational units, and that his treatment is not concerned with the ecological trends of character variation. In contrast, Sinskaja (1942) comes to the conclusion that "ecotypes are quite often connected with each other by a gradual series of transitional forms; the composition of a population then undergoes gradual changes from one ecotype to the other in a definite geographical direction or in an ecological series of habitats". She believes (1931, p. 58) that "continuity in the zonal variability is naturally formed in the course of the migration of the complex of types from one common focus in the direction of a gradual change in climate", and cites the ecotypic differentiation within Eurasian *Camelina* as an example of continuous variation. Since the form that this zonation assumes will help us to appreciate Sinskaja's conception of ecotypic groupings, we shall examine the *Camelina* example more closely.

Sinskaja and Beztuzheva (1931, fig. 6, p. 172) list four ecologically significant groups of *Camelina sativa*; *C. caucasica*, *C. linicola*, *C. glabrata* and *C. crepitans*, which, according to Turesson's definition, represent four ecotypes. These ecotypes are, however, by no means ecotypically homogeneous units, though they do illustrate the major ecotypic groupings within the area.

Camelina glabrata is not a sharply differentiated variational type but gradually becomes *C. sublinicola*, which in turn passes into *C. linicola*. Within *C. sublinicola* itself the forms nearer to *C. glabrata* than to *C. linicola* have been tentatively united under the name *C. sub-glabrata*. *Camelina caucasica* is also a composite

ecotypic group the component populations of which vary considerably in respect of the length of their vegetational periods. In Armenia *C. caucasica* occurs with forms very near to *C. sublinicola*; in fact it represents "a curious combination of the features of *C. glabrata* and *C. linicola*" (Sinskaja and Beztuzheva, 1931, p. 194). Finally there is *Camelina crepitans*, which occupies a position apart.

In contrast to the variational continuity illustrated by the major ecotypic groupings in *Camelina*, Sinskaja is of the opinion that where two ecotypes have spread from different foci so as to meet each other, the zones of variation become more clearly defined. Thus instead of variational continuity we find what she calls "zonal localisation".

Like Turesson, Sinskaja regards the "process of ecotype origination" as the criterion for the separation of different kinds of ecotypes. On this basis, *Camelina glabrata* is essentially a climatic ecotype, *C. linicola* and *C. crepitans* are phytosocial ecotypes, while *C. caucasica* owes its characteristics about equally to the action of both climatic and phytosocial selection. However, Sinskaja's climatypes (climatic ecotypes) are sometimes very comprehensive ecotypic populations covering very large areas indeed. For instance, in Black Mustard (*Brassica nigra*) she recognises a European climatype which covers Western Europe, Afghanistan, Abyssinia, Crete and Cyprus, and an eastern climatype which comprises two secondary climatypes—a Syrian and an Asia Minor climatype. Within the area of the latter secondary climatype she has delimited a synecotype, *i.e.*, a phytosocial ecotype.

Thus we have here an hierarchal system, a system of zonal and intra-zonal ecotypes. This hardly squares with the statement that "two ecotypes of one and the same species cannot exist in the same habitat", for, in the example just given, the synecotype, a habitat population, is not only part of a secondary climatic ecotype, but is also a local unit of the primary climatic ecotype. However, in certain cases, the classification of ecotypes within ecotypes simplifies recording, but it is obvious that unless ecotypic variation is to some extent discontinuous a phytosocial ecotype, for instance, could not be regarded as belonging to any climatype in particular.

Since it is not always clear for lack of breeding data whether the variation studied by Sinskaja and her co-workers is ecotypic or ecospecific, we shall now consider the altitudinal variation of the Californian population of *Potentilla glandulosa*, for which fertility data are available. Clausen, Keck and Hiesey (1941) recognise five climatic ecotypes in this area: a Coast Range ecotype recognised

taxonomically as sub-sp. *typica*, a Foothills ecotype, sub-sp. *reflexa*, a Midaltitude ecotype, sub-sp. *Hanseni*, a Sub-Alpine ecotype, and an Alpine ecotype which together compose sub. sp. *nevadensis*.

The plants of the Coast Range ecotype "have fundamental, morphological and physiological characteristics in common by which they may be distinguished from all other races" (1941, p. 238). But according to the diagram on p. 247, this ecotype is an independent unit separated spatially from its nearest neighbour the Foothill ecotype. The Foothill ecotype occurs from about 700 to 6800 feet elevation, but at the higher levels, where it overlaps the distribution of the Midaltitude ecotype, it is found exclusively on the warmest slopes. "A clear-cut ecological separation is maintained between the two", for the Midaltitude ecotype prefers moist cool meadow habitats and never grows on the dry hillsides, whereas the Foothill ecotype avoids the meadows. Since hybridisation is apparently limited to the actual contact zone, the Foothills ecotype is virtually another independent unit. On the other hand, in sub-species *nevadensis* the change from the Sub-Alpine to the Alpine ecotype is continuous.

Although these ecotypes are regarded by Clausen, Keck and Hiesey as climatic ecotypes, and from their data there is no doubt but that they are climatically differentiated, the fact remains that, in one case, distance prevents intergrading, and in another, the separation is occasioned by an abrupt edaphic change.

It is significant that Clausen *et al.* state that such regional climatic races "are most homogeneous towards the centre of their distribution but frequently intergrade through hybridisation where they meet or even overlap". Perhaps the observation refers more to the taxonomic characters than to the climatically controlled ones, for, if we examine the numerical data, we find that the taxonomic categories are themselves ecotypically differentiated in response to climate. In this connection the Sierran population of *Achillea millefolium* is worthy of our attention. The same authors (1946) examined samples from altitudes of about 1000 feet, 3000 feet and 11,000 feet. "In every sample taken a considerable array of individual variation was found, yet most populations were sufficiently distinct from the others to be readily recognised as statistically different" (p. 114). It should be noted that, unlike *Potentilla*, the differentiation of climatic races has here been achieved without any accompanying development of convenient taxonomic characters.

There is certainly nothing inevitable about the correlation of

taxonomic with ecotypic groupings, for in the Californian population of *Deschampsia caespitosa* Lawrence (1945) has shown that any correlations which may exist are largely incidental; in fact, he says "the distribution of its taxonomic variants appear to be entirely independent of any ecotypic adaptation" (p. 312).

From Lawrence's data the indication is that in *Deschampsia caespitosa* we again have an example of intra-ecotype differentiation. He recognises three Californian ecotypes, Coastal, Upper Montane, and Alpine: the first and the last are based on single collections taken at sea-level and at 10,000 feet respectively, but the Upper Montane population, tentatively regarded as a single ecotype, is represented by collections made at 6225 feet, 7200 feet and 8200 feet. Plants from 6225 feet are weaker when grown at 10,000 feet and slightly stronger at 4600 feet than plants from 7200 and 8200 feet; and again plants from 7200 feet apparently have a higher survival value when cultivated at 100 feet than those from 8200 feet. But in the case of *D. caespitosa* it is not quite clear where the demarcation line, if any, between the ecotypes actually occurs. There is no doubt, however, that Lawrence's data fully justify his remark that striking differences occur between races from widely separated geographic areas having distinct climates.

Incidentally, it is worth noting that Lawrence regards the above-mentioned *intra* Upper Montane populations as equivalents of Sinskaja's ecoelements. But surely this is founded on a misconception, for, according to Sinskaja (1942), ecoelements are variate classes such as growth-form types.

A point which Mayr (1942) mentions, and one which has a very direct bearing on the problem of classifying ecotypic variation, is that "the local environment very often affects conspicuously only a single character, such as pigmentation, which is correlated in desert mammals and larks with the colour of the soil, while other characters behave independently or else are correlated with an entirely different set of environmental factors" (p. 196).

Hovanitz (1940) gives a most interesting account of the ecological colour variation of the butterfly *Oeneis chryxus* in the arctic-alpine and upper Hudsonian life-zones of the high Sierra Nevada Mountains. In this butterfly the colour of the upper surfaces of the wings forms a continuous range from rather dark yellow-brown to yellow-white, and both a very dark yellow-brown race and a very pale yellow-white race are represented in California and Western Nevada. The only apparent environmental difference between the habitats of the two races is that of soil colour. Climatic effects can be

discounted, for both races "inhabit the same life-zone and the white race lives both north and south of the brown race (humidity decreases southward)" (p. 374).

"The rock in the northern and southern Sierra Nevada, where the white race is found, is predominantly a white granite. On the contrary, in the distribution area of the brown race, the central region, the mountain-tops are composed of dark red rock" (p. 374).

In a diagram Hovanitz shows the trend of colour variation in geographical sequence. Starting in the north we have the pale race, further south the populations become darker, until at the centre of the brown race white or light-coloured individuals are very rare. The brown race then continues southward without any apparent change until it meets the pale race, and here there is a very narrow zone of intergradation "showing the entire range of variation from the darkest to the lightest" (p. 371).

The absence of a definite zone of intergradation in the one case and its presence in the other is apparently no chance happening but is related to the nature of the soil gradient. The gradual variational change is associated with a gradual change in the percentages of the two rock types, whereas the rapid change occurs where the red and white rocks replace each other rather abruptly.

Another striking range of colour variation also following a rock-colour gradient is described by Test (1945) for the limpet *Acmaea scabra*, an eurytopic species, *i.e.* a species of wide ecologic tolerance. "Specimens located upon granite have a whitish ground colour marked by speckles of black, exhibiting a truly astonishing resemblance to the granite; those which have grown upon sand rock are sometimes nondescript in colour, as is the rock; those upon green chert have green predominant in their coloration" (pp. 403-4). Test attributes this colour differentiation to the selective elimination of conspicuous individuals by predators. Ecotypic trends of this kind and those, for instance, in *Achillea millefolium*, where physiologically differentiated latitudinal races are just as diverse as the altitudinal ones at the same latitude, present very real difficulties to the practical taxonomist.

We can infer from the fact that different kinds of ecotypes have been described, that the effects of the predominant selective agents can, to some extent at least, be singled out for individual study. If then, instead of regarding each population which occupies a distinctive habitat as an objective territorial ecotype in the way Turesson has done, we imagine the ecotype subjectively as an assemblage of more or less separated breeding communities with

a certain range, or it may be a discontinuous stage, of hereditary variation lying along a climatic gradient, or edaphic, or biotic or any other environmental gradient we may choose to examine, we would be preparing the way for a more detailed and critical analysis of the distribution of ecotypic variation than the present practice permits. Huxley's term *ecocline* (Huxley, 1938) can usefully be used to denote a series of ecotypic populations showing genetic gradation related to a particular environmental gradient. It follows therefrom that "a habitat population which belongs to a particular ecocline ecotype, by virtue of possessing certain characteristics, may at the same time share its ecotypic status with ecotypes on other ecoclines by virtue of carrying their characteristics in addition. Thus the number of times a given areal population can represent a range, or stage, on an ecocline depends on the number of independent and ecologically significant genotypic trends found crossing its territory" (Gregor, 1944, p. 28).

One of the advantages of the cline concept is, as Valentine (1941) points out, that "it allows correlation of a range of habitats with a range of varying forms". For instance, in his treatment of the *Viola Riviniana* population in Britain he has recognised two main groups, *nemorosa* of sheltered habitats and *minor* of exposed habitats, but between these groups there lies a series of forms (*intermedia*) and many intermediate habitats. Here, then, we have an ecocline with subsp. *nemorosa*, form *intermedia*, and subsp. *minor* representing three convenient reference ranges, or ecocline ecotypes. Similarly in the case of the Sierra Nevada butterfly, the pale and dark races are the ecocline ecotypes, or reference ranges of variation, related to a soil colour gradient. It is also worth noting that the individual colonies which contribute to the ecocline variation are apparently more or less genetically homogeneous, for Hovanitz mentions that "within a restricted population, however, the individuals are remarkably uniform and only very occasionally are atypical examples found" (p. 371). This suggests a colonial population structure which would tend to favour local, in contrast to regional, response to environmental selection.

The ecotype situation just described conforms very closely to that found in the sea plantain, *Plantago maritima* (Gregor, 1939, 1946). In this species the ecocline ecotype is also a subjective reference range of variation, and the constituent colonial populations are unmistakably individualistic in the characters which they exhibit. However, not all character trends can be related to observable environmental gradients, and those of doubtful ecological

relationship have been called *topoclinal*, whereon the *topotypes* appear as the topoclinal equivalents of ecoclinal ecotypes (Gregor, 1939). It is possible to have the same character varying topoclinally as well as ecoclinally, for as Böcher (1944) has shown, the variation in leaf size in *Veronica officinalis* is ecoclinal when followed from woods out into the open, but topoclinally northwards and eastwards in Europe.

As we have already observed, the ecoclinal concept implies the recognition of environmental gradients, and it perhaps needs stressing that until hereditary variation can be related to some observable environmental gradient, we have no means of distinguishing between ecotypic and topotypic variation. Since it would be obviously impracticable to define a gradient in terms of total environment, it follows that the ecoclinal ecotype is the product of the selective action not of the total habitat factors, but only of those which contribute to a particular gradient.

The ecocline, therefore, records differences in the expression of individual characters or groups of characters along particular gradients, and it is by a collective examination of ecoclines that the local combinations of character can be appreciated. By superimposing ecoclinal records for an area, it would be possible to map the general distribution of ecotypic variation. However, the actual form which the ecoclinal ecotype assumes—that is, whether or not the ecotype has a definite beginning or end—will almost certainly be influenced by other factors besides those characteristic of the gradient to which it is related. For example, in California different edaphic conditions and spatial relationships by affecting the breeding structures of *Potentilla glandulosa* interrupt what might otherwise be a continuous climatic ecocline. Moreover, homogeneous regional ecotypes can hardly be expected when an ecoclinal population is subdivided, as most populations are, into relatively small gamodemes or breeding communities, isolated or partially separated from each other by uncongenial habitats.

If, on the other hand, we adhere to the concept of the ecotype as a product of its total environment we would have to be prepared to regard each and every local community, and an ecoclinal ecotype may comprise a large number of local communities, as an ecotype, or at least as a potential ecotype, because it is improbable that any two communities of a species grow under exactly the same combination of environmental factors; hence the chances are that no two local populations are ecotypically identical except perhaps when they happen to belong to self-fertilising, or apomict species.

While it is true that ecotypes have most commonly been reported in cross-fertilising species, adaptive populations within self-fertilising species, or for that matter within apomictic species such as occur in the genus *Poa*, can also justifiably be regarded as ecotypes. In a local colony of an ecotype belonging to a cross-fertilising species the unit of selection is essentially the individual variate, whereas the unit of selection in the self-fertilising or apomict species is most likely to be a group of genetically similar individuals. But even in the cross-fertilising species there is a possibility that a local habitat community may contain elements or sub-populations which lead more or less independent lives. For instance, Sinskaja (1942), has suggested that different ecoelements, *e.g.* early and late maturity types, in the same population, may become partially isolated from each other on account of an incomplete coincidence in their flowering times, and Stapledon (1928) has produced a certain amount of evidence in support of this view.

Although such examples are probably rare in cross-fertilising plants, for flowering uniformity is usually a striking feature of these local populations, they nevertheless do suggest that group competition is not the prerogative of the self-fertilising species.

Some interesting points are raised by Aitken and Drake (1941) when they question the ecotype status of "varieties" of different times of maturity within the self-fertilising species *Trifolium subterraneum* in Australia. The basis of these doubts is that varieties have not been developed locally, but have in all probability been introduced from Europe pre-formed, and so genetically pure that further selection by the new environment is highly unlikely. Yet their evidence suggests that the selective effect of the Australian environment is not entirely negative, for the distribution of different maturity types, different "varieties", is not unrelated to the new environmental conditions. As a rule early types are found in the districts where the growing season is long, while "in intermediate districts several maturity types may co-exist, although in competition there is usually a tendency for a particular type to dominate in any one position". The evidence in favour of the selective action of the Australian environment is further strengthened when these authors add that "in a district of short climatic growing season, such local environments as river flats or irrigated fields allow the predominance of much later types".

The arrival in Australia of genetically stable races from Europe would seem to have no real bearing on the question whether the variation in maturity is, or is not, ecotypic. When any self-

fertilising species extends its territory by migrating from one environment to another, be it by human or other agency, the chances are that the migrants will represent one, or more than one, group of true-breeding individuals, and their establishment and ultimate success in a new area will depend on their fortuitous arrival in habitats congenial to growth and reproduction. The only criterion upon which we can judge ecotype status is that of finding a relationship between the prevailing distribution of variation, in the present case maturity variation, and an observed environmental gradient. Aitken and Drake have shown such a relationship to exist between the distribution of maturity and length of the growing season, and accordingly maturity variation is ecoclinal, and therefore ecotypic. But as some of the habitat populations, *e.g.* the intermediate ones especially, are genetically complex in so far as they contain more than one "variety", and since, as we have noted earlier, a variate class can only represent an ecotype when it happens to be the sole component of a habitat population, it is apparent that in these circumstances the different maturity "varieties" actually represent different constituents of an ecotypic population, or ecoelements in the sense of Sinskaja. Thus although the "varieties" provide the material for ecotypic selection they are not themselves ecotypes, except at the ecoclinal limits where extreme conditions happen to have favoured one maturity class to the exclusion of all others. In cross-fertilising plants, on the other hand, since it is accepted as inevitable that populations will be of mixed genetic constitution, lacking sexually independent variate classes, the "varietal" *versus* ecotype situation is less likely to arise.

Let us now imagine that only one of these maturity "varieties" of *Trifolium subterraneum*, instead of several, had found its way into Australia. From an examination of the habitats where it succeeded best, it might still be possible to establish its environmental preferences in relation to length of growing season. If this were done, it would be legitimate to regard the Australian population of *T. subterraneum* not only as monotypic, but as mono-ecotypic in respect of seasonal response. This procedure would be in keeping with the treatment accorded to the Sierran populations of *Potentilla Breweri*, *Artemisia Suksdorfii* and *A. Douglasiana* by Clausen, Keck and Hiesey (1940), who have shown that in so far as response to the chosen climatic (altitudinal) gradient is concerned, these populations are monoecotypic, being represented respectively by a coastal, an alpine, and an exceptionally plastic coastal-midaltitudinal ecotype.

An actual example of what can be expected when a population of

very restricted variability happens to be introduced into new territory is provided by the agricultural population of *Phalaris tuberosa* in Australia. "This grass as it is known in Australia was first grown from a small packet of seed at the Botanical Gardens, Toowoomba, Queensland, in 1884. It is probable that the majority if not all the samples of *P. tuberosa* which have been sown intentionally, have originated from the limited number of cross-fertilising plants grown at Toowoomba" (Trumble and Cashmore, 1934, p. 1). The grass of cultivation is adapted to areas of summer drought, but it is apparently undifferentiated ecotypically, though, like *Potentilla Douglasiana* in California, it is tolerant of a considerable range of conditions.

When dealing with such monotypic populations it is very difficult indeed to assess the adaptive characteristics which determine their ecological distribution. For instance, in the high fertility coastal districts of New South Wales a monotypic race of perennial ryegrass (*Lolium perenne*) grows extensively, but it is only when it is compared with material from a moister and cooler region, such as New Zealand, that its ecotypic status in Australia becomes apparent. Moonie (1934) found that, though similar in general type to the New Zealand material, the New South Wales population is at least three to four weeks earlier in seeding. In cultivated species maturity differences of this kind are often so important agronomically that for classificatory purposes they are sometimes used to the exclusion of other characters. For instance, in Sweden, the rules governing the certification of local strains of red clover require that a distinction be made between late, medium late and early types, but, as Åkerberg and Julén (1946, p. 591) very properly remark, "there are strains of the same earliness, that still differ in their practical value." From the standpoint of the present discussion this incomplete kind of classification, based on a single variable character, is of rather special interest, as it illustrates the principle of recording particular ranges of agro-ecotypic variation along an agro-ecocline, for in red clover differences in time of flowering happen to be most conspicuously related to different agronomic practices, or, in other words, to a "utility" gradient. Thus we have here what might well be just the initial step towards an agro-clinal classification of the species.

In conclusion it is tempting to suggest that instead of trying to define all intra-specific variation in terms of traditional taxonomy, a more detailed picture of the internal structure of species would be obtained by freely admitting that the classification of ecotypic

variation is a special-purpose one involving its own peculiar concepts and techniques. The need at the moment is to overcome the almost subconscious desire to resolve intra-specific variation into categories capable of being absorbed into the orthodox taxonomic system, and the current emphasis on the discontinuities in the distribution of ecotypic variation, rather than on the ecotypic trends, is perhaps only a reflection of this taxonomic undercurrent. It would, however, be totally wrong to end this review by leaving the impression that taxonomic and genecological researches are antagonistic; on the contrary they are mutually helpful. Nevertheless it is difficult to see how the results from such different approaches can well be integrated. That traditional taxonomic practice provides biology with its basic general-purpose classification is a fact all too often ignored by the critics of the morphological system. Therefore, rather than attempt to graft the genecological concepts on to the existing system, it would be more satisfactory to regard genecological classification as an independent, subsidiary and special-purpose classification designed to present a realistic picture of the distributional arrangement of intra-specific variation.

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REPORT OF THE ANNUAL CONFERENCE OF THE
CRYPTOGAMIC SECTION, 1946.

By C. E. FOISTER.

(Read 21st November 1946.)

The Cryptogamic Section of the Society held the Fifty-eighth Annual Conference in the Peebles district on 4th and 5th October 1946, with headquarters at the Waverley Hotel, Peebles. Two forays were held, the first on 4th October at Dawyck Estate, Stobo, by kind courtesy of Lieut.-Col. A. N. Balfour, when there was an attendance of twenty-nine, while the second was held at Glentress, Peebles, on 5th October, by courtesy of the Forestry Commission. Both these estates are heavily wooded, mainly by coniferous trees, though a very wide range of trees and shrubs exists at Dawyck, many of which were initially introduced by the late Lieut.-Col. F. R. S. Balfour. The weather on Friday 4th was cold but fine, and a very good collection was made of both parasitic and saprophytic fungi and of the agarics. The leader of the party, Dr. Malcolm Wilson, specially demonstrated forestry diseases, of which *Cronartium ribicola* on *Pinus monticola* was one of the most important. The foray on Saturday 5th was favoured by perfect weather, and eighteen enthusiasts attended. Forestry diseases were less evident here, though *Armillaria mellea* was noted on the butts of felled trees, and *Rhabdocline Pseudotsugae* on Douglas Fir was found to be causing considerable damage. As at Dawyck, the Coprini were conspicuously absent, no doubt due to the acid character of the substrate in these two estates. The agarics found were stated by Dr. Grainger to be acid-loving species.

An evening meeting was held at the Waverley Hotel, Peebles, on 4th October. Dr. Wilson, who was in the chair, gave a brief talk on the forestry diseases noted during the day at Dawyck, with special reference to *Cronartium ribicola* and *Rhabdocline Pseudotsugae*. Dr. J. Grainger followed with a description of the outstanding agarics collected during the day, and pointed out the relation of weather conditions, seasonal temperatures, and acidity of the substrate to the development of the fructifications (1). Dr. M. Noble discussed a book which had belonged to Robert Kaye

Greville, and which contained holograph notes made by him in 1818-19 preparatory to the publication of his *Flora Edinensis* (1824). This book was presented by her to the library of the Society. Special thanks should be recorded to Lieut.-Col. A. N. Balfour and to the Forestry Commission for access to their estates, and to Mr. A. A. Pearson, Dr. R. W. G. Dennis, Dr. J. Grainger and Dr. M. Wilson for identifying the more difficult species. While mosses were not specially collected, thanks are due to Mr. C. Gimingham and Mrs. Robertson for checking the identities of the few mosses listed below. The collected species of fungi and other cryptogams totalled 157, and of these the more outstanding or unusual species were:

AGARICS. *Dictyolus muscigenus*, *Exidia saccharina* var. *foliacea*, *Hygrophorus Wynniae*, *Omphalia philonotis*, *Plicatura crispa*, *Poria vaporaria*, *Russula Velenovskyi*.

RUSTS. *Coleosporium Petasites* on *Petasites palmatus*, *Puccinia Violae* on *Viola Riviniana*, *P. annularis* on *Teucrium Scorodonia*, *Pucciniastrum Epilobii* on *Epilobium angustifolium*, *Uromyces Genistae-tinctoriae* on *Genista anglica*.

OTHERS. *Cordyceps ophioglossoides* on *Elaphomyces granulatus*, *Keithia Tsugae* on *Tsuga canadensis*, *Lophodermium vagulum* on *Rhododendron* spp., *Rehmiellopsis abietis* on *Abies magnifica*, *Rhabdocline Pseudotsugae* on *Pseudotsuga taxifolia*, *Hormiscium pino-phylum* on *Taxus baccata*.

LIST OF CRYPTOGAMS COLLECTED.

FUNGI.

HYMENOMYCETES.

Aleurodiscus amorphus (Pers.) Rabenh. on *Abies pectinata* DC.

Amanita muscaria (L.) Fr.; *rubescens* (Pers.) Fr.

Armillaria mellea (Vahl) Quél.; *mucida* (Schrad.) Fr.

Bolbitius titubans (Bull.) Fr.

Boletus badius Fr.; *chrysenteron* (Bull.) Fr.; *erythropus* (Pers.) Quél.; *scaber* (Bull.) Fr.

Cantharellus aurantiacus (Wulf.) Fr. (= *Clitocybe aurantiaca* (Wulf.) Studer.); *cibarius* Fr.

Clavaria cristata (Holmsk.) Fr.; *rugosa* (Bull.) Fr.

Collybia butyracea (Bull.) Fr.; *fusipes* (Bull.) Berk.; *platyphylla* (Pers.) Fr.; *radicata* (Relh.) Berk.; *velutipes* (Curt.) Fr.

Corticium comedens (Nees) Fr.

Cortinarius cinnamomeus (L.) Fr.

Dacrymyces deliquescens (Bull.) Duby.

Dictyolus muscigenus (Bull.) Quél. on *Polytrichum aloides* Hedw.

Entoloma sericeum (Bull.) Fr.

Exidia saccharina Fr. var. *foliacea* (Bref.) Bres.

Flammula sapinea Fr.

Fomes annosus (Fr.) Cooke

- Galera hypnorum* (Schrank) Fr.
Hebeloma crustuliniforme (Bull.) Fr.
Hygrophorus coccineus (Schaeff.) Fr.; *Wynniae* B. & Br. (= *Omphalia Wynniae* (B. & Br.) Quél.).
Hypholoma Candolleianum Fr.; *fasciculare* (Huds.) Fr.
Inocybe geophylla (Sow.) Fr. v. *lilacina* Fr.
Irpex obliquus (Schrad.) Fr.
Laccaria laccata (Scop.) B. & Br.; also var. *amethystina* (Vaill.) B. & Br.
Lactarius glyciosmus Fr.; *piperatus* (Scop.) Fr.; *subdulcis* (Pers.) Fr.
Lepiota amianthina (Scop.) Fr.; *cristata* (A. & S.) Fr.
Marasmius Hudsonii (Pers.) Fr.; *hariolorum* (DC.) Quél.; *peronatus* (Bolt.) Fr.
Mycena alcalina Fr.; *pelianthina* Fr.; *pura* (Pers.) Fr.
Naucoria conspersa (Pers.) Fr.; *Cucumis* (Pers.) Fr. (= *Nolanea pisciodora* (Ces.) Fr.).
Nolanea staurospora Bres. (= *N. proletaria* Fr.).
Omphalia philonotis (Lasch) Fr.
Paxillus involutus (Batsch) Fr.
Pholiota erebia Fr.; *mutabilis* (Schaeff.) Fr.
Phylloporus rhodoxanthus (Schw.) Bres.
Plicatura crispa (Pers.) Rea on Beech Mast.
Polyporus amorphus Fr.; *betulinus* Fr.; *perennis* (L.) Fr.
Polystictus abietinus (Dicks.) Fr.; *versicolor* (L.) Fr.
Poria vaporaria (Pers.) Fr.
Psaliota arvensis (Schaeff.) Fr.
Psathyrella disseminata (Pers.) Fr.
Psilocybe semilanceata Fr. var. *caerulescens* Cke.
Radulum orbiculare Fr.
Russula cyanoxantha (Schaeff.) Fr.; *emetica* (Schaeff.) Fr.; *heterophylla* Fr.; *lutea* (Huds.) Fr.; *nigricans* (Bull.) Fr.; *Velenovskyi* Melzer and Zvara.
Stereum hirsutum (Willd.) Fr.; *purpureum* (Pers.) Fr.; *sanguinolentum* (A. & S.) Fr.
Stropharia aeruginosa (Curt.) Fr.; *semiglobata* (Batsch) Fr.; *stercoraria* Fr.
Tricholoma nudum (Bull.) Fr.; *rutilans* (Schaeff.) Fr.
Tubaria furfuracea (Pers.) W. G. Smith.

GASTEROMYCETES.

- Lycoperdon perlatum* Pers.
Phallus impudicus (L.) Pers.
Scleroderma aurantium Pers.

UREDINALES.

- Coleosporium petasites* Lév. on *Petasites palmatus* A. Gray; *Senecionis* Fr. on *Senecio vulgaris* L.; *Tussilaginis* Kleb. on *Tussilago Farfara* L.
Cumminsia sanguinea (Peck) Arthur on *Mahonia Aquifolium* (Gursh) Nutt.
Melampsora hypericorum Wint. on *Hypericum pulchrum* L.
Phragmidium violaceum Wint. on *Rubus fruticosus* L.
Puccinia annularis (Str.) Schlecht. on *Teucrium Scorodonia* L.
Puccinia Buxi DC. on *Buxus sempervirens* L.; *coronata* Corda on *Holcus mollis* L.; *graminis* Pers. on *Agrostis* sp.; *Violae* DC. on *Viola Riviniana* Reichb.
Pucciniastrum Epilobii Otth. on *Epilobium angustifolium* L.
Thecopsora myrtilli (Schum.) Hunter on *Vaccinium Myrtillus* L.
Uromyces Airae-flexuosi Ferd. & Wge. on *Aira flexuosa* L.; *Genistae-tinctoriae* Wint. on *Genista anglica* L.; *Pisi* Wint. on *Lathyrus pratensis* L.

ASCOMYCETES.

- Aleuria vesiculosa* (Bull.) Boud.
Calycella citrina (Hedw.) Quél.
Ciliaria scutellata (L.) Quél.
Claviceps purpurea (Fr.) Tul. on *Agrostis stolonifera* L. var. *gigantea* Koch
 (= *A. alba* L.), *Anthoxanthum odoratum* L., *Dactylis glomerata* L.,
Lolium perenne L., *Phleum pratense* L.
Cordyceps ophioglossoides (Ehrh.) Link on *Elaphomyces granulatus* Fr.
Dasyscypha calyciformis (Willd.) Rehm on *Pinus monticola*.
Diatrype stigma (Hoffm. ex Fr.) Fr.
Diatrypella quercina (Pers. ex Fr.) Cke.
Elaphomyces granulatus Fr.
Erysiphe Cichoracearum DC. on *Senecio Jacobaea* L.; *Graminis* DC. on *Poa*
 sp.; *Polygoni* DC. on *Lathyrus pratensis* L.
Fabraea ranunculi Fr. on *Ranunculus repens* L.
Helotium virgultorum (Vahl) Karst.
Hypoxyton multifforme Fr.
Keithia Tsugae (Farl.) Durand on *Tsuga canadensis* (L.) Carr.
Leotia lubrica (Scop.) Fr.
Lophodermium cladophilum (Lév.) Rehm on *Vaccinium Myrtillus* L.;
 vagulum Wils. & Robertson on *Rhododendron* spp.
Otidea leporina (Batsch) Fekl.; *onotica* (Pers.) Fekl.
Rehmiellopsis abietis (Rostr.) O. Rostr. on *Abies magnifica* Murr.
Rhabdocline Pseudotsugae Syd. on *Pseudotsuga taxifolia* (Poir.) Britt.
Rhytisma acerinum Fr. on *Acer Pseudoplatanus* L.
Sphaerella rhododendri Cke. on *Rhododendron* spp.
Stegia ilicis Fr. on *Ilex Aquifolium* L.
Uncinula Aceris (DC.) Sacc. on *Acer Pseudoplatanus* L.
Xylaria hypoxyton (L. ex Fr.) Grev.

PHYCOMYCETES.

- Bremia Lactucae* Regel on *Senecio Jacobaea* L.

FUNGI IMPERFECTI.

- Hormiscium pinophilum* (Nees ex Fr.) Lindau on *Taxus baccata* L.
Mastigosporium album Riess on *Alopecurus pratensis* L.
Ovularia obliqua (Cke.) Oudem. on *Rumex obtusifolius* L.
Ramularia Urticae Ces. on *Urtica dioica* L.
Sepedonium chrysospermum Fr.
Sporocybe Azaleae (Peck) Sacc. on *Rhododendron* buds.

While interest was concentrated on the fungi, the following mosses, etc., were also collected:—

MOSSES.

- Camptothecium sericeum* Kindb.
Catharinea undulata W. & M.
Dicranum scoparium Hedw.
Hylocomium splendens B. & S.; *triquetrum* B. & S.

Hypnum cupressiforme L. ; also var. *filiforme* Brid. on trunk of *Acer pseudo-platanus*.
Mnium undulatum L.
Polytrichum aloides Hedw. ; commune L.
Thuidium tamariscinum B. & S.

LIVERWORTS.

Frullania Tamarisci (L.) Dum.
Metzgeria furcata (L.) Dum. on trunk of *Acer pseudoplatanus*.
Plagiochila asplenioides (L.) Dum.

LICHENS.

Peltigera canina Willd.
Usnea barbata Web.
Xanthoria parietina Th.

ALGA.

Trentepohlia aurea (L.) Mart.

MYXOMYCETES.

Badhamia utricularis Berk.
Lycogala epidendrum Fr.
Trichia varia Pers.

REFERENCE.

- (1) J. GRAINGER. Ecology of the Larger Fungi. Trans. Brit. Mycol. Soc., xxix, 1/2, pp. 52-63 (1946).

HIGHER FUNGI OF WESTER ROSS. By R. W. G. DENNIS,
Royal Botanic Gardens, Kew.

(Read 12th December 1946.)

Apart from a few records from Loch Maree incorporated by the Rev. J. Stevenson in "Mycologia Scotica," there appear to be hardly any published accounts of the fungi of the province of Ross. During a fortnight spent in Applecross and on Gairloch in September–October 1946, the writer was agreeably surprised at the richness of the Agaric flora both as regards individuals and species. The following lists of species observed may perhaps be acceptable as a contribution to the knowledge of the higher mycoflora of the North-west Highlands, and it is hoped they may stimulate others to enter this neglected field of study. The old native pinewoods of Loch Maree seem particularly worthy of attention. Water-colour sketches were made of all species with which difficulty in naming was encountered, and in the majority of cases the specimens drawn were dried and are preserved in the herbarium of the Royal Botanic Gardens, Kew. Facilities for oven-drying a large number of agarics were kindly provided by the proprietrix of the Temperance Hotel, Applecross. It was thus possible to check determinations made in the field by microscopic examination of spores and cystidia after the specimens were received at Kew.

FUNGI OF LARCH WOODS.

All the records refer to Applecross, except a few from Gairloch (G).

Amanitopsis fulva (Schaeff.) W. G. Sm.

Lepiota amianthina (Scop.) Fr.

Tricholoma aurantium (Schaeff.) Fr. (G); *rutilans* (Schaeff.) Fr.

Mycena galopus (Pers.) Fr.; *sanguinolenta* (A. & S.) Fr.

Clitocybe nebularis (Batsch.) Fr. (G).

Laccaria laccata (Scop.) B. & Br.

Russula ochroleuca (Pers.) Fr.; *emetica* (Schaeff.) Fr.; *drimeia* Cke.; *vesca* Fr.

Lactarius rufus (Scop.) Fr.; *subdulcis* (Pers.) Fr.; *turpis* (Weinm.) Fr.

Nolanea cetrata (Fr.) Schroet.

Cortinarius stemmatus Fr.; *semi-sanguineus* (Brig.) Maire (G).

Astrosporina lanuginella Schroet.; *lanuginosa* (Bull.) Schroet.

Galera hypnorum (Schränk) Fr.

Paxillus involutus (Batsch) Fr.

Stropharia aeruginosa (Curt.) Fr.

Hypholoma fasciculare (Huds.) Fr.

Psalliota sylvicola (Vitt.) Fr.

Poria candidissima (Schw.) Sacc. (= *P. hymenocystis* B. & Br.); *sanguinolenta* (A. & S.) Fr.

Tomentella fusca (Pers.) Schroet.

Peniophora glebulosa (Fr.) Bres.; *byssosidea* (Pers.) v. Hohn. & Litsch.

Clavaria inaequalis (Mull.) Quél.

Tremella mesenterica (Retz.) Fr. (on Gorse).

Calocera viscosa (Pers.) Fr. (G).

ADDITIONAL SPECIES UNDER PINE.

Mycena ammoniaca Fr.

Russula Queletii (Fr.) Bataille; *coerulea* Cke.

Pholiota flammans Fr.

Pleurotus porrigens (Pers.) Fr. (Shieldaig).

Boletus variegatus (Swartz) Fr. (G); *bovinus* (L.) Fr. (G).

Coniferous plantation at Slumbay, Loch Carron, yielded the following additional species:—

Cortinarius purpurascens Fr.; *lepidopus* Cke.; *cinnamomeus* (L.) Fr. var. *crocifolius* Peck.

FUNGI OF BIRCH WOODS.

All the records refer to Applecross (mixed Birch-Hazel scrub), except some from South Shore of Loch Torridon (T) and Loch Maree (M).

Amanita virosa Fr.; *muscaria* (L.) Fr. (T); *rubescens* (Pers.) Fr. (T).

Armillaria mellea (Vahl) Fr.

Tricholoma fulvum (DC.) Fr. (M).

Laccaria laccata (Scop.) B. & Br.; also var. *amethystina* (Vaill.) B. & Br.

Collybia maculata (A. & S.) Fr. (T).

Omphalia umbellifera (L.) Fr.

Lactarius subdulcis (Pers.) Fr.; *vietus* Fr. (Applecross and T); *camphoratus* Fr.; *insulsus* Fr.; *torminosus* (Schaeff.) Fr. (T); *vellereus* Fr. (M).

Russula fallax (Schaeff.) Fr. (T); *fragilis* (Pers.) Fr.; *emetica* (Schaeff.) Fr.; *ochroleuca* (Pers.) Fr.; *foetens* (Pers.) Fr.

Cantharellus cibarius Fr. (T); *tubaeformis* Fr.

Nolanea staurospora Bres.

Cortinarius triumphans Fr. (T); *anomalus* Fr.; *caninus* Fr.; sp. near *fasciatus* Fr.

Pholiota mutabilis (Schaeff.) Fr. (M).

Hebeloma crustuliniforme (Bull.) Fr. (T).

Tubaria furfuracea (Pers.) W. G. Sm.

Stropharia aeruginosa (Curt.) Fr.

Hypholoma fasciculare (Huds.) Fr.

Panaeolus campanulatus (L.) Fr.

Boletus scaber (Bull.) Fr. (T).

Hydnum repandum (L.) Fr. (T); also var. *rufescens* (Pers.) Fr. (T).

Polyporus betulinus (Bull.) Fr. (Applecross and T).

Fomes fomentarius (L.) Fr. (M).

FUNGI OF LOWLAND PASTURE, BELOW 200 FEET
ABOVE SEA-LEVEL.

The records are from Applecross, except a few from Loch Ewe
and Gairloch (G).

Lycoperdon umbrinum Pers. (L. Ewe).

Lepiota gracilentia (Krombh.) Fr. : *amianthina* (Scop.) Fr.

Tricholoma melaleucum (Pers.) Fr.

Hygrophorus laetus (Pers.) Fr. ; *virginus* (Wulf.) Fr. ; *russocoriaceus* Berk. & Miller (Applecross and G) ; *pratensis* (Pers.) Fr. ; *conicus* (Scop.) Fr. ; *puniceus* Fr. ; *coccineus* (Schaeff.) Fr. ; *psittacinus* (Schaeff.) Fr. ; *chlorophanus* Fr. ; *sciophanus* Fr.

Omphalia umbellifera (L.) Fr.

Mycena flavo-alba Fr. (G).

Entoloma sericeum (Bull.) Fr. ; *porphyrophaeum* Fr.

Leptonia sericella (Fr.) Quél.

Inocybe geophylla (Sow.) Fr. (G, park land).

Galera tenera (Schaeff.) Fr.

Annellaria separata (L.) Karst.

Stropharia semiglobata (Batsch) Fr.

Panaeolus campanulatus (L.) Fr.

Clavaria vermicularis Fr. ; *corniculata* (Schaeff.) Fr. (G).

Geoglossum atropurpureum Pers. ex Fr. ; *nigritum* Cke. (L. Ewe) ; *glutinosum* Pers. ex Fr. (L. Ewe) ; *Cookeianum* Nannfeldt (= *G. glabrum* sensu Durand non Pers.) (G, sand-dunes).

Crepidotus mollis (Schaeff.) Fr. occurred on a living ash-tree at Applecross, *Coprinus atramentarius* (Bull.) Fr. under oak at Gairloch, and *Psilocybe elongata* (Pers.) Fr. amongst sphagnum on the moors between Loch Ewe and Gruinard Bay.

The writer's thanks are due to Mr. A. A. Pearson for determining a number of agaric species and checking many more, to Miss E. M. Wakefield for naming the *Porias* and *Thelephoraceae*, and to Professor J. A. Nannfeldt for checking the *Geoglossums* and for detecting *G. glutinosum* among the collection of *G. nigritum* made by the roadside between Loch Ewe and Gruinard Bay.

ADDITIONAL RECORDS MADE IN JUNE 1947.

Amanitopsis vaginata (Bull.) Roze. Under oak, Toscaig. 11.6.47.

Collybia extuberans (Batt.) Fr. On heap of pine sawdust, Shildaig. 4.6.47.

Marasmius dryophilus (Bull.) Karst. Very abundant under bracken, Shildaig and Applecross.

M. esculentus (Wulf.) Karst. On buried Scots pine cones, Shildaig. 3.6.47

M. androsaceus (L.) Fr. On dead heather, Shildaig. On dead *Scirpus caespitosus*, 1000 ft., Applecross Moor. 12.6.47.

Mycena alkalina v. *chlorinella* Lange (= *M. metata* sensu Kühner non Lange).

Amongst grass under birch, Shildaig. 6.6.47.

Amongst grass under hawthorn, Applecross. 10.6.47.

- M. vitilis* Fr. sensu Lange non Kühner. On fallen oak twigs, Applecross. 12.6.47.
- Hygrophorus vitellinus* Fr. On bare peat, 2000 ft., on Meall Gorm. 12.6.47.
- Omphalia fibula* v. *Swartzii* Fr. Applecross. 12.6.47.
- O. sphagnicola* Berk. In sphagnum tussock on moor, 800 ft., Applecross. 12.6.47.
- O. umbellifera* (L.) Fr. Abundant up to 1100 ft., Applecross. 12/13.6.47.
- Panus stipticus* (Bull.) Fr. On birch stump, Shieldaig. 6.6.47.
- Russula cyanoxantha* Fr. Under oak, Applecross. 12.6.47.
- R. heterophylla* Fr. Under oak, Toscaig. 11.6.47.
- Entoloma clypeatum* (L.) Fr. Amongst grass under hawthorn, Applecross. 11.6.47.
- Nolanea cetrata* Schroet. In sphagnum, 1200 ft., on Ben Shieldaig. 5.6.47.
- N. staurospora* Bres. forma. Sandy pasture, Applecross. 11.6.47.
- This appears to be the short, dark form recorded by Lange from a coastal common in Denmark and regarded by him as equivalent to *N. proletaria* in the sense of Ricken. Its spores appear identical with those of normal *N. staurospora*.
- Pholiota praecox* (Pers.) Fr. Sandy pasture at head of Applecross Bay. 9.6.47.
- Inocybe flocculosa* Berk. v. *abjecta* (Karst.) Heim. Amongst grass in willow and birch scrub, Shieldaig. 6.6.47.
- Naucoria semiorbicularis* (Bull.) Fr. Amongst grass with *Pholiota praecox* and *Stropharia coronilla*, Applecross. 9.6.47.
- Galera hypnorum* (Schrank) Fr. Amongst moss in birch woods, Shieldaig. 6.6.47.
- Tubaria pellucida* (Bull.) Fr. sensu Lange. On peaty soil by roadside, 600 ft., Applecross. 12.6.47.
- Bolbitius vitellinus* (Pers.) Fr. Amongst grass by roadside, Applecross. 10.6.47.
- Stropharia coronilla* (Bull.) Fr. Sandy pasture, Applecross. 9.6.47.
- Hypoloma Candolleianum* Fr. Around stump of frondose tree, Applecross. 10.6.47.
- H. chondrodermum* (B. and Br.) Lange. On rotting coniferous log, Applecross. 12.6.47.
- H. fasciculare* (Huds.) Fr. On logs, Applecross. 12.6.47.
- Anellaria separata* (L.) Karst. Applecross. 12.6.47.
- Psilocybe bullacea* (Bull.) Fr. On acid sandy soil under heather, Upper Loch Torridon. 3.6.47.
- Panaeolus sphinctrinus* Fr. Sandy pasture between Applecross and Toscaig. 11.6.47.
- Psathyra spadiceogrisea* (Schaeff.) Fr. sensu Lange. Under hawthorn, Applecross. 10.6.47.
- Psathyrella caudata* Fr. sensu Lange. Clustered at base of hawthorn trunk, Applecross. 12.6.47.
- **Coprinus Martinii* Favre. On *Scirpus caespitosus*, Shieldaig. 2.6.47.
- C. micaceus* (Bull.) Fr. Around stumps, Toscaig. 10.6.47.
- C. plicatilis* (Curt.) Fr. Very abundant in grass along roadside between 250 and 600 ft., Applecross. 12.6.47.
- Polyporus squamosus* (Huds.) Fr. Abundant on ash and sycamore, Applecross. 12.6.47.
- P. brumalis* (Pers.) Fr. On rotting logs (already old by 10.6.47), Applecross.
- Pistillaria cardiospora* Quélet. On rotting *Caltha palustris*, Toscaig. 11.6.47.
- Exobasidium Vaccinii* (Fckl.) Woron. On *Vaccinium myrtillis*, Shieldaig. 6.6.47.

- Corticium subcoronatum* v. Höhn and Litsch. On pine chip, Shieldaig. 10.6.47.
- C. (Gloeocystidium) polygonium* (Pers.) Fr. On dead branch of white poplar, Applecross. 11.6.47.
- Tremella albida* (Huds.) Fr. On oak twigs, Applecross. 12.6.47.
- T. mesenterica* (Retz.) Fr. On gorse, Applecross. 10.6.47.
- **Exidia repanda* Fr. On birch branches, Shieldaig. 5.6.47.

GASTEROMYCETES.

- Rhizopogon luteolus* Fr. Under pine, Shieldaig. 4.6.47.
- Bovista nigrescens* Pers. Sandy pasture at head of Applecross Bay. 13.6.47.

HYPOCREACEAE.

- Cordyceps gracilis* Mont. and Dur. On buried caterpillars amongst bracken, Ben Shieldaig. 5.6.47.

* New to Britain.

THE GENUS PRIMULA: SECTION VERNALES Pax.

By W. WRIGHT SMITH and H. R. FLETCHER.

(Read 15th May 1947.)

The section Vernaless was constituted by Pax (1) in 1889 in his preliminary survey of the genus *Primula* and his choice of title was an apt one. He had before him five species with several varieties on which to found his brief diagnosis which runs as follows: "Folia revolutiva, membranacea, rugosa, plus minus pubescentia, efarinosa, indivisa, in petiolum plus minus alatum contracta vel sensim attenuata, serrulata vel denticulata vel crenulata. Flores lutei vel purpurascens, in umbellam dispositi, saepe nutantes scapo elongato vel subnullo. Bracteae involucrales non gibbosae, angustae. Calyx tubulosus vel campanulatus, laciniis acutis. Capsula cylindrica, exserta vel calyce inclusa." The distribution of the section, as given by Pax at that date, differs in no respect from that of the present day. It includes the whole of Europe except the subarctic, Asia Minor, the Urals and Caucasus, Armenia, Persia, and eastwards as far as the Altai; one species occurs in Algiers.

In 1905 in his Monograph Pax (2) added nothing to his previous diagnosis nor to the distribution, but recorded eight species for his section, expressing doubt, however, whether two of them merited specific rank. The most important addition was *P. Juliae* which with its suborbicular cordate leaves presented a strong contrast in facies. Pax had no material of it, but quite correctly followed Kusnetzow (3) in assigning it to Vernaless. In the content for Vernaless given in 1928 by Smith and Forrest (4) at the Fourth *Primula* Conference there are only minor changes in the Paxian fabric. They enumerate six major species, for the two which were suspect to Pax, *P. pseudoelatoria* and *P. heterochroma*, are relegated to the position of subspecies. Certain units, accorded but varietal rank by Pax, are also placed among the subspecies. In the list formulated by Harrison (5) after an exhaustive series of hybridisation experiments on the members of the section, *P. Pallasii* and *P. Lofthousei* are assigned specific status while *P. leucophylla* is subordinated to *P. elatoria* as a subspecies. His arrangement therefore contains seven major aggregates.

This conflict of opinion does not, however, preclude a large measure of agreement. But it must be recognised that many of the subspecies and even some of the varieties have in the past received diagnoses as species, and in many publications are still deemed to merit this higher status. In the present review no marked deviation from the approximate consensus (as outlined above) has been attempted. The aim has been to assemble all the relevant literature and to place the data in such a way that the problems involved can be readily envisaged. The number of major aggregates is thus restricted to six—not far removed from the Paxian treatment. (Be it understood, however, that this somewhat arbitrary arrangement does not carry the implication that those who favour a larger number of specific units for the section are in the wrong. Standards vary and will continue to vary.) The only alteration of any significance is the inclusion of *P. megaseaefolia*. For a long time the locus of this species was in doubt. Referred by Pax (2) (*l.c.*, 45) to *Carolinella*, a Chinese section with which it has no affinity whatever, it was made the sole member of a section *Megaseaefolia* by Balfour (6), and retained in that category by Smith and Forrest (4) (*l.c.*, 27) in proximity to *Vernales*. Later cytological investigations on it were carried out by Harrison (*l.c.*, 74) and by Bruun (7) and these have served to elucidate the problem. But the cytology of *Vernales* as a whole should first be referred to.

The section shows a marked uniformity in its cytological data. In all cases—in species, subspecies, and hybrids— $2n=22$, as has been demonstrated by Harrison (*l.c.*, 74) and by Bruun (*l.c.*, 124). As regards size of chromosome and configuration, Bruun (*l.c.*, 40) finds nothing comparable except in *P. megaseaefolia*. This species and the *Vernales* form a distinctly delineated cytological type. "The conclusion is therefore quite obvious that *Vernales* and *Megaseaefolia* constitute a separate branch of the genus, so far removed from other sections that no kinship with any other group can be demonstrated cytologically. The close coincidence between these two sections is rather surprising, because *P. megaseaefolia* in its orbicular petiolated leaves greatly differs from the *Vernales* type." The morphological diversity from the *Vernales*, as noted by Bruun, is only a little more pronounced in *P. megaseaefolia* than what is found in *P. Juliae*, the affinity of which with the *Vernales* has never been in doubt. Thus with reinforcement from the cytology, a further scrutiny of the general features of *P. megaseaefolia*, particularly the structure of the calyx and of the corolla and the abundant articulate hairs, favour its inclusion in *Vernales*. The

extent to which members of the section can be successfully hybridised is well indicated in the experiments recorded by Harrison (*l.c.*, 75). He has attempted to hybridise *P. megaseaefolia* with *P. vulgaris* but, although seeds were produced, they did not germinate (Harrison in litt.). (*P. megaseaefolia* is rare in culture, not very amenable and a very early flowerer, but when conditions permit, crossing with *P. Juliae* is an experiment worthy of further trial.

If cytology gives no clue to the affinities of the Vernales, the morphological features are equally indecisive. Though certainly not closely akin, certain sections such as Obconica and Cortusoides, which possess articulate hairs and no farina, are not entirely alien. The section has no direct link with the species of China, Japan, and the Himalaya, and the Asiatic members of it keep a northern line through the Caucasus to the Altai. But in contrast with the European section Auricula, the Vernales have a strong Asiatic representation. In spite of the wide range of the section in Europe there is a greater diversity in the West Asian region. Long ago Pax (1) (*l.c.*, 177) was of opinion that the major development of the section took place there. On this subject Stapf (8) has a pertinent note, pointing out that the Russian botanist Grossheim (9) refers *P. heterochroma* to his group of autochthonous Hyrcanian species, relics of an eastern old Mediterranean centre which extended throughout the Pontic region, the Caucasus, and the southern Caspian Province, the Hyrcania of the Ancients. In the same note Stapf adduces the work of Troll, who in dealing with Oceanic elements in the flora of Central Europe claims for *P. vulgaris* the character of a eu-atlantic-mediterranean-montane species.

The brief history of the section itself has already been outlined, but the history of the three common European components of the section goes far back not only in botanical literature but in the language of nearly every country in Europe. The term *Primula* began to be restricted to members of the genus (as now understood) in the time of the herbalists in the middle of the sixteenth century. But the word appeared some centuries earlier. Thus in 1101 in *Regimen Sanitatis Salerni* in a list of plants supposed to cure paralysis occurs *Primula veris*. (This is late Latin without any counterpart in the classical Latin authors.) But the name implies the "little firstling of spring", and was not the undisputed possession of any primrose, for the daisy among others was one of the claimants. As for *primrose*, it is not found in Chaucer or in Gower but is recorded in late Middle-English by 1413, corresponding in form to early Old

French *primerose* and late Latin *primea rosa*. The popular title *cowslip*, according to the New English Dictionary, can be traced at least to A.D. 1000 as *cu slyppan* and *cusloppe*. Cognate names are in other Teutonic languages.

The Vernales are also concerned with the earliest observations on heterostyly. The discovery of heterostyly is usually attributed to Sprengel in 1793 for *Hottonia* and to Persoon in 1794 for *Primula elatior*. But recently Van Dijk (10), in an article entitled "La Découverte de l'Hétérostylie chez *Primula* par Ch. de L'Écluse et P. Reneaulme", has brought evidence to show that the phenomenon was not unknown to Clusius and clearly appreciated by Reneaulme. Clusius (11), in dealing with what are now members of section *Auricula* observes: "flores . . . stilo inter stamina nonnunquam prominente, interdum autem nullo." Apparently, however, he did not realise that heterostyly was the usual condition in *Primula*, for he refers to one species (now *P. Clusiana*) as having a prominent style and to another (now *P. minima*) as lacking a prominent style. (Obviously, as Van Dijk suggests, his collections of these showed only the one phase.) Reneaulme in 1611 had before him (under terms of his own) *P. veris*, *P. vulgaris*, and a hybrid between them. It is clear that the difference in length of style was noted by him, and he employed the expression "Macrostylos" as opposed to "Anostemon." As his book is not available at the present time a citation from Van Dijk must serve: "Non seulement le style long du 'Macrostylos', et les anthères visibles dans la gorge de la fleur du 'Anostemon' (d'où ce nom), mais encore les étamines courtes du premier, et le style court, ainsi que l'insertion des étamines dans la partie supérieure du tube de la corolle du dernier sont mentionnés." The explanation of these heteromorphic flowers had to await the investigations of Darwin (12). The terms 'pin-eyed' and 'thrum-eyed' for the two conditions have been current for a hundred and fifty years in this country—perhaps much earlier—among gardeners devoted to *Auriculas* and *Polyanthus*, but a search in the horticultural literature before 1800 has failed to disclose evidence of a prior usage.

The natural hybrids of the section are discussed under the species concerned. There is, however, a large and important group of garden hybrids which merits more than a brief mention. These are the *Polyanthus Primulas*. At one time they were the dominant members of the genus in culture in this country and still occupy a prominent place. They are developments from crosses between *P. veris* and *P. vulgaris*. The normal colour in these two species is yellow, but in the wide range of *P. vulgaris*, particularly in

England, France, and the Orient, red, mauve, and purple tints appear, while *P. veris* has also coloured forms. These variations in colour, as well as double forms, were known in culture to botanists and herbalists before the end of the sixteenth century. It was in England that most interest was taken in them, and for long they were termed on the Continent "English Primroses". There is no evidence that these early coloured Primroses and Cowslips were hybrids. But about the middle of the seventeenth century considerable progress had been made in the production of many varieties of "Polyanthus". The most authoritative account of the origin and history of the Garden Polyanthus is in a publication by Miller Christy (13). In his view there are three possible and indeed probable explanations of the origin—not inconsistent with one another. Firstly, the crosses may have been effected under natural conditions where at least one of the coloured forms was native and the cultivator removed the most promising results to his garden. Secondly, as coloured forms were already in culture, there was ample opportunity there for hybridisation. As Christy puts it (p. 21), there may have been a garden origin as well as a wild origin. Thirdly, shortly before 1635 there was introduced from the Orient to France *P. vulgaris* var. *rubra* (=subsp. *Sibthorpii*), and before 1640 into England. This bright-red "Turkey Primrose" became at the time very popular in English gardens and almost certainly played a considerable part in the evolution of Polyanthus. In the Monograph of Pax (p. 65) the assemblage of forms of this hybrid is referred to under the general term *P. anglica* Pax—a contraction from a somewhat similar usage dating from Lobelius and from Bauhin.

In contrast with *Auricula*, where the content and the status of the species are practically stable, the widely distributed *Vernales* offer much more of a field for differences of opinion as to the position of the various units. The occurrence of one or more members of the *Vernales* in every country in Europe has resulted in a great mass of literature on the section. Botanists of each country—or even of each province or county—for more than three hundred years have contributed their views on the section in general or with particular reference to individual species in their various habitats. It has therefore been impracticable to assemble all the references to members of the section. The citations given under each species, subspecies, or variety are still fairly ample. In this selection the aim has been to quote all the important treatises (even those dealing with single species), also those publications which include plates or figures, and wherever possible books of ready access.

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KEY TO THE SPECIES OF SECTION VERNALES.

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| A. Leaves longer than broad, never orbicular: | |
| B. Scape obsolete | <i>P. vulgaris</i> |
| BB. Scape well developed, with several flowers: | |
| C. Corolla limb flat: | |
| D. Colour of corolla dominantly yellow | <i>P. elatior</i> |
| DD. Colour of corolla dominantly shades of purple (Turkey, Asia Minor, and Caucasus) | <i>P. amoena</i> |
| CC. Corolla limb concave | <i>P. veris</i> |
| AA. Leaves $\pm$ orbicular, about as broad as long (Asia Minor and Caucasus): | |
| B. Scape obsolete | <i>P. Juliae</i> |
| BB. Scape well developed with several flowers | <i>P. megaseaeifolia</i> |

P. amoena M. Bieb., Fl. Taur. Caucas., I, 138 (1808), excl. var. β ; Lehmann, Monogr. Primul., 39, t. 3 (1817), excl. var. β .; Bot. Mag., t. 3252 (1833); Ruprecht in Bull. Acad. Sc. Pétersb., vi, 223 (1863), excl. var. β .; Boissier, Fl. Orient., iv, 26 (1879) *pro parte*; Journ. Roy. Hort. Soc., vii, 245, 268-9, 276, 278-9, 293 (1886); Pax in Engl. Bot. Jahrb., x, 180 (1889); Gard. Chron., vii, 175, 206, 271, 486 (1890); Sommier et Levier in Act. Hort. Petrop., xvi, 333 (1901); Kusnetzow in Acta Hort. Jurjev., ii, 156 (1901), and in Fl. Cauc. Crit., iv, 66 (1901); Pax in Engl. Pflanzenr. Primulaceae, 53 (1905); Gard. Chron., li, 33, 98 (1912); Journ. Roy. Hort. Soc., xxxix, 101, 167, 171-2 (1913); Farrer, Eng. Rock Gard., ii, 110 (1919); MacWatt, Primulas of Europe, 13, 32 (1923); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 42 (1928), and in Journ. Roy.

Hort. Soc., liv, 21 (1929); Harrison in Trans. North. Nat. Un., i, 48, 49, 74 (1931); Grossheim, Flora Kavkaza, iii, 205 (1932); Gard. Chron., xcix, 6, fig. 2 (1936); *ibid.*, c, 443 (1936); Journ. Roy. Hort. Soc., lxi, 409, 411, 423, fig. 116 (1936); *ibid.*, lxiii, 244, proc. p. lxvi (1938); Quart. Bull. Alp. Gard. Soc., ii, 214, fig. opp. p. 212 (1934); *ibid.*, iii, 156 (1935); *ibid.*, iv, 108, 113, 120, (1936); *ibid.*, xi, 202, fig. p. 203 (1943); W. W. Sm. in Bot. Mag., t. 9593 (1940). *P. amoena* var. *genuina* Pax in Engl. Bot. Jahrb., x, 180 (1889), and in Engl. Pflanzenr. Primulaceae, 53 (1905)—*pro parte*. *P. elatior* Ledeb., Fl. Ross., iii, 9 (1847–49) *pro parte*. *P. elatior* var. *amoena* Duby in DC. Prodr., viii, 36 (1844); Ledeb., Fl. Ross., iii, 9 (1847–49); Regel in Acta. Hort. Petrop., iii, 133 (1874). *P. elatior* var. *dubia* Regel in Gartenfl., xxv, 258, t. 877a (1876). *P. elatior* × *amoena* Pax in Engl. Bot. Jahrb., x, 183 (1889). *P. altaica* Hort.

The first specimens of this species were secured from the Caucasus by M. Bieberstein, who in his diagnosis associated it with *P. elatior*. He included in it an acauline variety which was known later as *P. Sibthorpii* Hoffmannsegg (otherwise *P. vulgaris rubra*). *P. amoena* is found throughout the Caucasus and extends into Armenia and Lazistan in N.E. Turkey. It is recorded at various elevations from 1000 m. up to nearly 4000 m., where it flowers near the melting snow on peaty banks and on broken rock amid *Rhododendron* and *Vaccinium* scrub. Like its ally *P. elatior* it is a variable plant, and some half-dozen varieties or forms have been described showing divergences in height, in shape of leaf and degree of hairiness, in the number and size of the flowers, in colour of corolla and in length of capsule. Its affinity to *P. elatior* is undoubted, and at times it has been assessed as a subspecies or variety of that widespread species. It must be admitted that the chief distinction is the colour of the flower, which in *P. elatior* is almost consistently yellow while in *P. amoena* some shade of violet-blue or purple predominates.

The typical plant was introduced into cultivation first at St. Petersburg (now Leningrad) and later at Edinburgh, where it flowered in 1833 and was figured for the Botanical Magazine (t. 3252). It continued in culture intermittently, but the record is difficult to decipher owing to confusion with *P. Sibthorpii*. It was effectively reintroduced some twelve years ago by Balls from the Trebizond district of Turkey and opportunity taken for a more adequate figure in Bot. Mag. (t. 9593), where an account is given of its

vicissitudes in culture. It is hardy out of doors in Britain but far from common.

A perennial herb with the habit of *P. elatior*, and with a fairly short stout rhizome from which spring numerous fleshy roots. Leaves only partially developed when the flowers open, when mature 5–16 cm. long, including the petiole; lamina 3–8 cm. long, 2–4 cm. broad, spatulate-oblong, elliptic or oblong, rounded at the apex, usually tapering but sometimes truncate or subcordate at the base, irregularly crenate or denticulate at the margin, upper surface bright green and glabrous or slightly hirsute at or near the mid-rib., densely covered with white wool below but in some forms glabrescent; mid-rib and 6–9 pairs of lateral nerves slightly impressed above, prominent below; petiole 2–8 cm. long, membranously winged, finely hirsute to glabrescent. Scape 5–15 cm. tall, slender or fairly stout, as a rule markedly hirsute, carrying an umbel of 2–18 flowers, usually 6–10; bracts 2–8 mm. long, linear-lanceolate, hirsute; pedicels 0.5–4 cm. long, more or less erect, hirsute to glabrescent. Calyx 8–12 mm. long, tubular, strongly 5-nerved so as to be almost pentagonal, glandular-pubescent especially along the nerves, cut to a quarter or a third into ovate to lanceolate, acute or obtuse, markedly ciliate lobes. Corolla brilliant violet-blue or lavender-blue tinged with red or a clear pale mauve, very rarely white, with a yellow eye, exannulate, heteromorphic, slightly glandular-puberulous on the outside; tube as long as or twice as long as calyx, narrowly cylindrical, amplate above insertion of stamens; limb 1.5–2.5 cm. in diameter with patent obcordate deeply emarginate lobes. Stamens, with anthers 1.5 mm. long, inserted near middle of corolla-tube in pin-eyed flowers, slightly below apex of tube in thrum-eyed. Long style as long as or almost as long as corolla-tube; short style half as long as corolla-tube. Capsule up to 1.5 cm. long, oblong, often well exserted from the calyx, dehiscing by apical teeth. Seeds 1 mm. in diameter, resembling those of *P. elatior* but somewhat smaller.

Reference has already been made to the variability of the species in the field. In 1863 Ruprecht (*l.c.*) described *P. Meyeri*, which subsequent commentators generally preferred to rank as a variety or subspecies of *P. amoena*. Kusnetzow (*l.c.*), who travelled widely in the Caucasus and collected *P. amoena* from many localities, recognised six varieties of which var. *Meyeri* is one. It is evident from a short paper written by Kusnetzow (*l.c.*, 156) that a fellow-botanist, Lipsky, had challenged the validity of these varieties. In his reply Kusnetzow gives further morphological and geo-

graphical data on his varieties without claiming for them a definite stability. Shortly afterwards in Fl. Cauc. Crit. (*l.c.*) the same author gives full diagnoses of his varieties with elaborate notes. In his Monograph Pax (*l.c.*), who had material of most of the varieties, upheld five of them and related the sixth to his own var. *genuina*. In a comparatively recent enumeration of the Caucasian flora Grossheim (*l.c.*) follows Kusnetzow and makes no reference to Pax. Without ample material from the Caucasus there can be no warrant to deviate from the analysis made by Kusnetzow. His varieties are accordingly detailed below, with the pertinent literature, to which has been added their distribution in the provinces of the Caucasus as given by Grossheim (*l.c.*). A tentative key is appended.

KEY TO VARIETIES OF *P. AMOENA*.

A. Leaves tomentose below:

B. Blade decurrent:

C. Leaf-margin minutely denticulate var. *Kasbek*

CC. Leaf-margin grossly bidentate var. *sublobata*

BB. Blade cordate or truncate:

C. Blade abruptly contracted at base but not cordate var. *grandiflora*

CC. Blade cordate var. *hypoleuca*

AA. Leaves glabrescent below:

B. Blade abruptly contracted; 1-3-flowered var. *Meyeri*

BB. Blade decurrent; many-flowered var. *intermedia*

var. **grandiflora** Kusn. in Del. I. Plant. exsicc., 25 (1898), and iii, 65 (1900); Acta Hort. Jurjev., i, 69 (1900); ii, 157 (1901); Fl. Cauc. Crit., iv, 69 (1901); Pax in Engl. Pflanzenr Primulaceae, 54 (1905); Grossheim, Fl. Kavkaza, 1, iii, 205 (1932).

North Caucasus.

var **hypoleuca** Kusn. in Del. III. Plant. exsicc., 65 (1900); Acta Hort. Jurjev., *l.l.c.*; Fl. Cauc. Crit., *l.c.*; Pax in Engl. Pflanzenr, *l.c.*; Grossheim, *l.c.*

Georgia.

var. **intermedia** Kusn. in Acta Hort. Jurjev., ii, 159 (1901); Fl. Cauc. Crit., *l.c.*; Pax in Engl. Pflanzenr., *l.c.*; Grossheim, *l.c.*

North Caucasus, Abkhazia, and Georgia.

var. **Kasbek** Kusn. in Del. III. *l.c.*; Acta Hort. Jurjev., *l.l.c.*; Fl. Cauc. Crit., *l.c.*; Grossheim, *l.c.*

North Caucasus and Georgia.

var. **Meyeri** (Ruprecht) Boiss. Fl. Orient., iv, 26 (1879); Pax in Engl. Bot. Jahrb., *l.c.* and in Engl. Pflanzenr., *l.c.*; Sommer et Levier in Acta Hort. Petrop., xvi, 333 (1900); Kusnetzow in Del. III., *l.c.*; Acta Hort. Jurjev., *l.l.c.*; Fl. Cauc. Crit., *l.c.*; Grossheim, *l.c.* *P. amoena* M. Bieb. var. *minuta* Kusn. in Del. I. Plant. exsicc., 24 (1898). *P. amoena* M. Bieb. var. *glabrescens* Akinf. in Alp. Plant. Central Cauc., p. 26, ex Kusnetzow. *P. amoena* M. Bieb. subsp. *Meyeri* (Ruprecht) W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 42 (1928), and in Journ. Roy. Hort. Soc., liv, 21 (1929); Harrison in Trans. North. Nat. Union, i, 49 (1931). *P. Meyeri* Ruprecht in Bull. Acad. St. Pétersbourg, vi, 224 (1863); Regel in Acta Hort. Petrop., iii, 130 (1874).

North Caucasus, Abkhazia and Georgia.

var. **sublobata** Kusn. in Del. III. Plant. exsicc., 65 (1900), and in Acta Hort. Jurjev., *l.l.c.*; Fl. Cauc. Crit., *l.c.*; Pax in Engl., *l.c.*; Grossheim, *l.c.* *P. amoena* var. *genuina* Pax in Engl. Bot. Jahrb., x, 180 (1889)—*pro parte*. *P. Mnischeikii* Bayern in sched. ex Kusnetzow.

North Caucasus and Georgia; also Lazistan ex Pax.

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Primula elatior has been known in Europe for some centuries. Its record in botanical and other literature, along with that of its close allies *P. veris* and *P. vulgaris*, belongs to the early history of the genus. The very old popular names did not discriminate it from these two species. It was, however, figured by Brunfels in 1534 (Contrafayt Kreuterb.). By 1583 its present name was already foreshadowed. Clusius (Rarior. aliquot stirp., p. 339) included under *P. veris* sive *Herba paralysis* the three species and also *P. farinosa*, our plant being distinguished as *P. veris, flore pallido, elatior*. In 1753 Linnaeus continued to regard the three Vernales species as one specific unit embracing three varieties. But very soon after, as appears from the publications of Hill, of Schreber and of Jacquin, *P. elatior* was assigned specific status.

P. elatior, if interpreted broadly to include several subspecies, has a very wide distribution in Europe and Asia. It is found throughout Europe, reaching Denmark and South Sweden as its northern limit. In Asia it appears in the Urals, the Caucasus, Armenia, Persia, and as far as the Altai. In England and in Denmark it occurs almost at sea-level, and in the Alps may ascend to 2600 m. As is the case with *P. veris*, its extensive territory assembles a surprising number of deviations, great and small, from what may be taken as the normal plant, that of Central Europe. These have been assessed as species, subspecies, varieties and forms. The literature dealing with the plant is profuse and names have multiplied exceedingly. The botanists of nearly every country concerned have added their quota. It is true that this is due in some measure to the detailed analysis to which the plant has been subjected for nearly two hundred years—as well as to the conflicting

opinions of mankind. But the major factor doubtless has been the colonising power of the ancestral species, or aggregate if you will. However, in spite of the complexity, the time devoted to *P. elatior* should have brought about some degree of stability as to the general framework. To that end by far the most valuable advance is the Monograph of Pax (*l.c.*), whose treatment of the Vernales has been generally accepted and is not likely to suffer any material modifications. He divided *P. elatior* into five varieties, left his *P. leucophylla* outwith it, and also with hesitation *P. pseudoelatior*. The careful analysis of Lüdi (*l.c.*) supported Pax in so far as the Primulas of Central Europe were concerned. In the list given by Smith and Forrest (*l.c.*) five subspecies (including *P. pseudoelatior*) appear under *P. elatior*, while *P. leucophylla* is excluded. In the review by Harrison (*l.c.*) the subspecies quoted are *leucophylla*, *Ruprechtii*, *carpatica*, *cordifolia*; *P. Pallasii* is retained as a species, with *P. intricata* and *pseudoelatior* as subspecies; *P. Lofthousei*, a recent addition, has specific status. Thus in the last half-century the numbers and the validity of the units remain practically unchanged. The problem is the status to be assigned to each unit. Complete agreement is unlikely, and the present authors have no warrant to decide the issue.

Even in his day Lehmann (*l.c.*) ends his dissertation on *P. elatior* thus: *Aliae in variis libris descriptae varietates levissimae, non attendendae, loci natalis conditione aliisque rebus degeneratae sunt et quotidie adhuc oriuntur.* And a hundred years later Pax (*l.c.* 48) confesses: *Varietates et formae supra descriptae areas geographicas discretas habitant, certis limitibus vix definiendae sunt et aegre inter se distinguuntur.*

The geographical criteria are the main resource, for the morphological data overlap in a perplexing way. The results of genetical analysis are also available, but these, though they may show differences, are not an exact measure of the status to be accorded to each unit. The conclusion is that no one unit in the aggregate of *P. elatior* has any clear claim to *precedence* over the others. The major components, apart from that of Central Europe, which is taken as typical, are therefore treated as subspecies. In view of their past history, it may tend to lucidity if they are thus kept together. For their discrimination the geographical distribution is of major moment, as the morphological data are scarcely adequate in themselves. Nearly all of them have at one time or another been regarded as species, but not with general acceptance nor without challenge.

It will be expedient to deal fully in the first place with typical *P. elatior*—the *P. elatior* subsp. *genuina* (Pax) Lüdi. It is found throughout the middle belt of Europe, including the south of England, north and Central France, Denmark, south of Sweden, Germany, the northern Alps to the Carpathians, and south Russia. A detailed description is appended (p. 419), from which it is pertinent to emphasise that the leaves are oval or oblong, wrinkled below and grey-green but not tomentose, usually abruptly contracted into the petiole but not cordate, sometimes however attenuate; the hairs are $\frac{1}{4}$ – $\frac{3}{4}$ mm. long, stiff; calyx 10–15 mm. long; corolla-limb 1.5–2 cm. across.

Its occurrence in Britain is much restricted. It is found in certain small areas in East Anglia—in the counties of Essex, Suffolk, Cambridge, Hertford, Huntingdon, and Norfolk. It has also been recorded from Corbridge in Northumberland by Harrison (*l.c.*), but with the caveat that there it may be adventitious. Statements as to its existence in other English areas are all almost certainly erroneous owing to confusion with the very common hybrid which obtains between *P. veris* and *P. vulgaris*. The distribution in East Anglia has been very fully worked out and mapped by Miller Christy (*l.l.c.*), who stated that it is found exclusively on the Chalky Boulder Clay and is calciphilous, at least in Britain, where it hybridises freely with *P. vulgaris* but rarely with *P. veris*. He adduces evidence that its area is undergoing a steady contraction, as the plant is being “hybridised out of existence by the aggressive *P. vulgaris*”. (For further references on these points see Adamson in *Trans. Bot. Soc. Edin.*, xxiv, 85 (1912); Hill in *New Phytologist*, vi, 162 (1907); Christy in *ibid.*, xxii, 233 (1923); Lüdi in *Hegi, Illus. Fl. Mitt.-Eur.*, v, 3, 1748 (1927).)

A hairy perennial with a fairly stout long or short rhizome, girt at the apex with the broad withered basal remains of old foliage; furnished with numerous fibrous roots. Leaves, including the petiole, 5–20 cm. long, 2–7 cm. broad, ovate to elliptic or oblong, rounded at the apex, usually abruptly contracted at the base into the winged petiole, sometimes more gradually tapering at the base, crenate to denticulate, often erosely so, at the margin, rugose with the nerves impressed above and prominent below, pubescent above or glabrescent, pilose below, with hairs $\frac{1}{4}$ – $\frac{3}{4}$ mm. long; petiole usually subequal to lamina, sometimes a little shorter, membranously winged, occasionally with small auricles, broad and sheathing at the base, pilose. Scape 10–30 cm. tall, stiff and erect, pilose especially towards the apex, carrying a many-flowered secund

umbel of more or less drooping flowers; bracts 3-5 mm. long, linear, attenuate, pilose; pedicels 5-20 mm. long, pilose. Calyx 10-15 mm. long, tubular, 5-angled, pilose, cut to a third or to nearly a half into narrowly lanceolate acute to acuminate lobes. Corolla pale buff-yellow with a darker mark at base of each petal, exannulate, heteromorphic; tube a little longer than calyx, or nearly twice as long, cylindrical, ampliate above insertion of stamens; limb 1.5-2 cm. diameter, flat, with obcordate emarginate lobes. Stamens, with anthers 1.5 mm. long, inserted at middle of corolla-tube in pin-eyed flowers, at apex of tube in thrum-eyed. Long style as long as corolla-tube, short style half as long. Capsule as long as calyx or half as long again, cylindrical, dehiscent by apical teeth. Seeds about 1.5 mm. in diameter, in shape like those of *P. veris*, dark brown to blackish, finely vesicular-surfaced or warty.

In the area held by typical *P. elatior* in Europe, certain minor divergences have been observed and usually assessed as varieties or forms. Of these the following have received definite names:

form. **acaulis** Petermann, Fl. Lips. Excurs., 170 (1838); Pax, *l.c.*; Lüdi, *l.c.*

A form with the scape obsolete or nearly so, occurring here and there with the normal plant.

form. **albiflora** Stelzh. ex Lüdi, *l.c.*

A form with whitish flowers growing on basalt in Bohemia.

form. **calycida** Schube in 81 Jahres. Schles. Gesellsch., 60 (1904); Pax (*l.c.*); Lüdi, *l.c.*

A form with calyx cut to the base. Recorded from Silesia.

form. **colorata** Pax, *l.c.*; Lüdi (*l.c.*). *P. elatior* var. *rubrofusca* Lamotte, Fl. Plat. Centr. France, 514 (1881)?

A horticultural form with red flowers.

form. **dialypetala** Petermann, Deutsch. Flora, 460 (1849); Pax, *l.c.*; Lüdi, *l.c.*

An abnormal form with the corolla very deeply 5-partite. Appearing rarely along with the typical plant.

var. **diaphana** Domin, Sitzber. Kgl. Böhm. Ges. Wiss., No. lviii, 38 (1903), and in Act. Bot. Böhem., x, 179 (1931); Lüdi, *l.c.*

The leaves are glabrous, as is the scape, elliptic-obovate, thin and translucent, with long broadly-winged petiole; calyx narrowly

tubular-campanulate, with long pointed triangular lobes; corolla pale yellow: capsule equalling calyx. Reported from Bohemia in deep pine-forests.

form. **fragrans** (E. H. L. Krause) Pax, *l.c.*; Lüdi, *l.c.* *P. fragrans* E. H. L. Krause in Ber. Deutsch. Bot. Ges., ii, 171 (1884); Domin., *l.c.* 179 (1931)—*pro var.*

A form with deep-yellow fragrant flowers, from localities in N. Germany. The typical plant is usually said to have no scent or very little.

var. **Lingelsheimii** Pax in Jahrb. Schles. Ges. Vaterl. Kultur, lxxxvi, IIb, 27 (1909); Fedde, Repert. Nov. Spec., viii, 93 (1910).

According to Pax, this Mecklenburg variety differs in its shorter more campanulate calyx and in its yellowish-green corolla with rather erect acute mucronulate lobes.

form. **mirabilis** Celakovsky in Sitzb. Kgl. Böhm. Ges. Wiss. Prag, 1888, 482 (1889); Pax, *l.c.*; Lüdi, *l.c.*

An autumn-flowering state from Bohemia with smaller flowers, hardly the size of those of *P. veris*.

var. **obscura** Harrison in Trans. North. Nat. Union, i, 52 (1931).

Leaves dark grey-green with pronounced pubescence. Recorded by Harrison from Essex, Saxony, Switzerland, and the Pyrenees.

form. **Perreiniana** (Flügge) Pax, *l.c.*; Lüdi, *l.c.* *P. elatior* var. *Perreiniana* Flügge ex Pax in Engl. Bot. Jahrb., x, 179 (1889). *P. Perreiniana* Flügge in Ann. Mus. d'Hist. Nat. Paris, xii, 420, t. 37 (1908); Duby in DC. Prodr., viii, 36 (1844); Willkomm et Lange, Prodr. Fl. Hisp., ii, 638 (1870). *P. Flüggeana* Lehmann, Monogr. Prim., 36, t. 2, excl. var. β (1817).

In this garden form the calyx of the purple flowers is cut almost to the base. Flügge's description and figure are based on plants grown in S. France, collected near Corunna in Spain and alleged to be wild. Lehmann (*l.c.*) claims to have found it in the mountains

near Bassano in Italy. In his Monograph (*l.c.*) Pax notes that the monstrosity was figured by Volkamer in 1708!

form. **rotundata** Boas in Mitteil. Bayer. Botan. Gesellsch., ii, 421 (1912); Lüdi, *l.c.*

The corolla-lobes in this form are semi-orbicular and entire.

form. **Schoenmanniana** Boas (*l.c.* cum fig.); Lüdi, *l.c.*

Here the corolla-lobes are widely emarginate with a tooth or aciculus in each sinus.

form. **Schusteriana** Boas (*l.c.* cum fig.); Lüdi, *l.c.*

A form with the corolla-lobes deeply and narrowly emarginate.

form. **uniflora** Petermann, Fl. Lips. Excurs., 170 (1838); Hennings in Schrift. Naturw. Ver. Schlesw.-Holst., ii, 185 (1876): Pax, *l.c.*; Lüdi, *l.c.*

A form with the scape bearing only a single flower.

In addition to the variations noted above there is a further concourse of names to be found in Acta Botanica Böhémica, x, 178 (1931), where Domin gives a very detailed analysis of *P. elatior* as it occurs in Bohemia. Some of the titles are resuscitations from the century-old work of Opiz and some are newly coined by Domin. Many deal with minutiae of little significance. In certain cases the chosen epithet is sufficient explanation, while in others a geographical term for variety or form indicates a local divergence which may or may not occur elsewhere. It is expedient to quote Domin's list in full. Items marked by an asterisk are dealt with elsewhere in the text. For the others reference can be made to Domin's publication.

P. elatior var. *communis* f. *macropus* (*elatior communis longipes*); f. *macrantha*; f. *stenantha*; f. *acaulis* *; f. *mirabilis* *; f. *uniflora* *; f. *rotundifolia*; f. *grandifolia*; f. *glabriuscula*; var. *diaphana* *; var. *fragrans* *; var. *brachycalyx* *; var. *montana* *; var. *danubialis* *; var. *purpurea* with f. *simplex*, f. *plena*, f. *calycantha*; var. *corcontica*; var. *acutidens*; var. *tatrensis* with f. *holoptera* and f. *longipes*; var. *carpatica* * with f. *polonensis*; var. *Schuriana* *; var. *Benköiana* *.

KEY TO THE SUBSPECIES OF *P. ELATIOR*.

- A. Leaves cordate or abruptly contracted:
 - B. Leaves glabrous (Caucasus) *cordifolia*
- BB. Leaves $\pm$ hairy:
 - C. Leaves green below not tomentose:
 - D. Leaves oblong (Central and N. W. Europe) *elatior*
 - DD. Leaves $\pm$ rotundate-ovate (Carpathians) *carpathica*
 - CC. Leaves tomentose below, not green:
 - D. Leaves cordate (Caucasus) *pseudoeelatior*
 - DD. Leaves rotundate-ovate (Carpathians) *carpathica*
- AA. Leaves gradually attenuate at base:
 - B. Leaves glabrous (Caucasus to Altai) *Pallasii*
- BB. Leaves tomentose or pubescent:
 - C. Leaves tomentose below (white or grey):
 - D. Leaves fugitively tomentose; calyx 6-8 mm. (Carpathians) *leucophylla*
 - DD. Leaves persistently tomentose; calyx $\pm$ 1 cm. (Caucasus) *Ruprechtii*
 - CC. Leaves hairy or finely pubescent below (green):
 - D. Leaves with stiff hairs, $\frac{1}{4}$ - $\frac{3}{4}$ mm. long:
 - E. Leaves oblong (Central and N.W. Europe) *elatior*
 - EE. Leaves $\pm$ rotundate-ovate (Carpathians) *carpathica*
 - DD. Leaves with very fine pubescence:
 - E. Calyx 10-12 mm. long (Pyrenees and S. Europe to Balkans) *intricata*
 - EE. Calyx 12-20 mm. long (Sierra Nevada) *Lofthousei*

P. elatior subsp. **carpathica** (Fuss) W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 42 (1928), and in Journ. Roy. Hort. Soc., liv, 21 (1929); Harrison in Trans. North. Nat. Union, i, 49, 65, 74, (1931). *P. carpathica* (Griseb. et Schenk) Fuss, Fl. Transsylv., 534 (1866); Simonkai, Enum. Fl. Transsylvan., 459 (1886); Roemer, Pflanzenwelt Burzenländ. Sieben-Bürg., 64, t. 14 (1898); Ungar, Alpenfl. Südkarpath., t. 17, fig. 2 (1913). *P. elatior* var. *carpathica* Griseb. et Schenk in Wiegmann's Arch., 320 (1852); Schneider et Sagorski, Fl. Central Karp., ii, 381 (1891); Pax in Engl. Pflanzenr. Primulaceae, 50 (1905); Journ. Roy. Hort. Soc., vii, 277, 279 (1889); *ibid.*, xxxix, 101, 223 (1913); Lüdi in Hegi Ill. Fl. Mittel-Eur., v, 1748 (1927); Quart. Bull. Alp. Gard. Soc., v, 307 (1937). *P. elatior* var. *carpathica* et var. *Schuriana* Domin et var. *Benköiana*, Domin in Act. Bot. Bohem., x, 181 (1931). *P. elatior* var. *carpathica* f. *subarctica* (Schur) Pax, *l.c.* *P. subarctica* Schur in Österr. Bot. Zeitschrift, xi, 359 (1861). *P. elatior* Baumgarten, Enum. Fl. Transsylv., i, 134 (1816); Fuss, *l.c.*; Heuffel in Verh. Zool. Bot. Ges. Wien, 187 (1858); Schur, Enum. Pl. Transsylv., 552 (1866). *P. elatior* var. *transsylvanica* Winkler in Österr. Bot. Zeitschr., xvi, 46 (1866). *P. alpestris* Schur in Verh. Siebenbürg. Vereins Naturw., iii, 89 (1859)—*nomen*. *P. intricata*

Janka in Linnaea, xxx, 590 (1859-60). *P. crenata* Salzer, Reisebilder Siebenbürgen, 323 (1860). *P. montana* Schur, Enum. Pl. Transsylv., 553 (1866). *P. elatior* var. *carpathica* f. *Benköiana* (Borbas) Pax, l.c. *P. Benköiana* Borbas in Termesztudományi Közlöny, ii, Pötfüz. (1888). *P. elatior* var. *villosula* Pax in Österr. Bot. Zeitschr., xlvii, 194 (1897). *P. Columnae* Schur, Enum. Pl. Transsylv., 554 (1866). *P. oblongifolia* Schur, l.c., 555 (1866).

In his very brief description Fuss (l.c.) notes that the rugose crenulate leaves are subrotundate-ovate and somewhat villous; also that the calyx teeth are ovate-acuminate. But he adds the caveat: *Planta viva habitu peculiari distinctissima sed characteribus diagnosticis aegre a P. elatiore discernenda*. Assessed in the first place by Grisebach and Schenk as a variety, it was so viewed by both Pax and Lüdi. The latter (l.c.) comments on the broad short-stalked finely indented leaves and the somewhat inflated calyx. The plant is confined to the Carpathians. In the Central Carpathians the leaves are less villous and almost green below—f. *subarctica*. It occurs on limestone in the East Carpathians with leaves grey-tomentose below—f. *Benköiana*. Generally this subspecies is more robust than typical *P. elatior*, is more hairy and more inclined to rotundity in the lamina of the leaf. From its Carpathian associate, subsp. *leucophylla*, it deviates in leaf-shape, in the much winged petiole and in the longer calyx.

P. elatior subsp. **cordifolia** (Rupr.) W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 42 (1928), and in Journ. Roy. Hort. Soc., liv, 21 (1929); Harrison in Trans. North. Nat. Union, i, 49 (1931). *P. cordifolia* Ruprecht in Bull. Acad. St. Pétersbourg, vi, 225 (1863); Sommier et Levier in Act. Hort. Petrop., xvi, 332 (1900), including var. *ovalifolia* Sommier et Levier; Grossheim, Fl. Kavkaza, iii, 206 (1932). *P. elatior* var. *cordifolia* (Rupr.) Pax in Engl. Bot. Jahrb., x, 179 (1889); Kusnetzow, in Act. Hort. Bot. Univ. Imp. Jurjev., i, 68 (1900), and in Fl. Cauc. Crit., iv, 62 (1901); Pax in Engl. Pflanzenr. Primulaceae, 51 (1905); Journ. Roy. Hort. Soc., xxxix, 101, 168, 171, 172 (1913). *P. Meyeri* var. *cordifolia* Regel in Act. Hort. Petrop., iii, 130 (1874). *P. Pallasii* var. *cordifolia* Boiss. Fl. Orient., iv, 26 (1879).

The criteria relied on by Ruprecht, Kusnetzow and Pax to distinguish this plant may be summarised thus: Leaves ovate-

rotundate, cordate at the base, subglabrous, not rugose, abruptly contracted into a petiole longer than the blade, unwinged or very narrowly winged; calyx very narrowly tubular with very narrow lobes.

To these points it may be added that the petiole is sometimes distinctly winged but evenly so from apex to base, can be twice as long as the blade and reach 10–12 cm.; the blade measures 4–7 cm. long, 4–5 cm. broad.

The plant is a native of the Caucasus and of Armenia, at elevations of 1300–2100 m. It differs from subsp. *pseudoelatio* in its almost glabrous habit; from subsp. *Pallasii* and subsp. *Ruprechtii* in its cordate leaves.

P. elatior subsp. **intricata** (Godron et Gren.) Lüdi in Hegi, Ill. Fl. Mittel-Eur., v, 1748 (1927); W. W. Sm. et Forrest in Notes Roy. Bot. Gard. Edin., xvi, 42 (1928), and in Journ. Roy. Hort. Soc., liv, 21 (1929). *P. intricata* Godron et Gren. Fl. France, ii, 449 (1852); Willkomm et Lange, Prodr. Fl. Hisp., ii, 637 (1870); Cusin, Herb. Fl. Franç., xv, t. 7 (1874); Kerner, Sched. ad Flor. Exsicc. Austro-Hung., iv, 45 (n. 1369) (1886); Journ. Roy. Hort. Soc., vii, 170, 269 (1886); Beck in Ann. Naturhist. Hofm. Wien, ii, 126 (1887); xiii, 6 (1898); Farrer in Engl. Rock Garden, ii, 144 (1919); Journ. Roy. Hort. Soc., lii, 158, 163 (1927); Javorka and Csapody, Ic. Fl. Hungar., 391 (1932); Gard. Chron., cii, fig. 162 (1937); Quart. Bull. Alp. Gard. Soc., iv, 92 (1936); *ibid.*, vi, 2, 13 (1937); *ibid.*, x, 167, fig. p. 166 (1942); *ibid.*, xiii, 13 (1945). *P. elatior* var. *intricata* (Godron et Gren.) Pax in Engl. Bot. Jahrb., x, 179 (1889)—*pro parte*; Widmer, Eur. Art. Prim., 128 (1891); Velenovsky, Fl. Bulgar., 477 (1891); Suppl. I, 242 (1898). *P. Pallasii* subsp. *intricata* (Godron et Gren.) Harrison in Trans. North. Nat. Union, i, 49, 56, 65, 74 (1931). *P. elatior* Beck in Ann. Naturhist. Hofm. Wien, ii, 144 (1887). *P. pachyscapa* Goiran, Spec. Morphogr., 35 ex Caruel in Parl. Fl. Ital., viii, 614 (1889). *P. rhododendricola* Sennen in Bull. Soc. Bot. France, lxxiii, 673 (1927)—*nomen*.

From the original description, based on plants collected in the Vallée d'Eynes and other places in the Eastern Pyrenees, the following data may be cited: Leaves green and very finely pubescent on both sides, oblong, obtuse, feebly or very irregularly crenulate even to the base, gradually narrowed into a long petiole with a

broad wing becoming obsolete below; scape, pedicels, and calyx with a fine tomentum; capsule equalling calyx.

This subspecies deviates from typical *P. elatior* in its smaller habit, in the decurrent, narrower and less wrinkled leaf-blades thickly beset with very short hairs. In facies it recalls the glabrous subsp. *Pallasii*. Its nearest of kin is the Sierra Nevada subsp. *Lofthousei*, which is much more robust with longer leaves and a larger calyx. Subsp. *intricata* may be said to replace *P. elatior* along the European side of the Mediterranean, occurring at 1600–2000 m. from the Pyrenees through the Southern Alps to the northern mountains of the Balkans. It has been in culture in this country for over sixty years and is amenable.

P. elatior subsp. **leucophylla** (Pax) Harrison in Trans. North. Nat. Union, i, 49, 65–67, 74–76 (1931). *P. leucophylla* Pax in Österr. Bot. Zeitschr., xlvii, 194 (1897), and in Engl. Pflanzenr. Primulaceae, 53, fig. 23B (1905); Engl. and Drude, Veget. Erde, x, II, 55 (1908); Journ. Roy. Hort. Soc., xxxix, 171 (1913); *ibid.*, xlv, proc. p. xxxii (1919); Hayek, Pflanzend. Oest.-leng., i, 425 (1915); Gard. Chron., lxxvii, 203 (1920); Prodan, Flora Determ. & Descr. Pl. Romania, ii, t. 100 (1923); Macwatt, Prim. Eur., 26, fig. facing p. 25 (1923); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 42 (1928), and in Journ. Roy. Hort. Soc., liv, 21 (1929); Farrer, Engl. Rock Garden, ii, 149 (1929); Javorka and Csapody, Ic. Fl. Hungar., 390 (1932); Bruun, Cytological Studies in Primula, 38, 124 (1932). *P. leucophylla* var. *longipes* Pax, l.c.

In the description of Pax the pertinent points appear to be the following: Leaves rugose, subcoriaceous, oblong or elliptic, crenulate or subentire, grey-tomentose below, gradually contracted into a narrowly winged petiole often as long as the blade which is 4–6 cm. long, 3–5 cm. wide, but increasing after flowering. Scape pubescent, 10–15 cm. high, but more in fruit. Calyx 6–8 mm. long, pilose; lobes lanceolate, acute, very short.

The plant is found on limestone formations in the East Carpathians—in the Bukovina and Transsylvania growing at 1600–1900 m. Pax associated the Carpathian plant with the Caucasian *P. Ruprechtii*, making the former var. *longipes* and the other var. *Ruprechtii*. The difference between them in length of petiole as adduced by Pax is in no wise convincing. The two diagnoses of Pax and Kusnetzow afford little in the way of contrast. The two

plants are well separated geographically and have never been regarded as identical. Subspecies *leucophylla* has apparently a more fugitive tomentum on the under-side of the leaf and a shorter calyx. Specimens cultivated at Edinburgh are more long-lived than other Vernales and show a very dense and persistent tomentum on the scape. This condition does not accord with the data of Pax and may be fortuitous.

P. elatior subsp. **Lofthousei** (Harrison) W. W. Sm. et Fletcher, Comb. nov. *P. Lofthousei* Harrison in *Vasculum*, xv, 75 (1929), and in *Trans. North. Nat. Union*, i, 49, 66, 74, 75, 76 (1931). *P. hispanica* Wilmott in *Journ. Bot.*, lxvii, 149 (1929). *P. intricata* Willkomm et Lange, *Prodr. Fl. Hisp.*, ii, 637 (1870)—*pro parte*, quoad plantas nevadenses. *P. elatior* var. *intricata* Pax in *Engl. Bot. Jahrb.*, x, 179 (1889), and in *Engl. Pflanzenr. Primulaceae*, 51 (1905)—*pro minima parte*, quoad plantas nevadenses. *P. intricata* var. *nevadensis* Font Quer in *Cavanillesia*, i, 21 (1928).

This plant is a native of the Sierra Nevada in the south of Spain. The first mention of it in literature as a distinct unit would appear to be by Font Quer (*l.c.*), who collected it in the fruiting stage in August 1923 at Puerto del Lobo at 2100 m. altitude. He attached his plant to *P. intricata* as a variety, giving a very brief description from which may be cited: Scape up to 35 cm.; leaves 12–30 cm. long; corolla-limb much shorter than tube (? *ex fructu*); capsule equalling calyx, inflated at base, ovoid-elongate.

Further collections were made in 1926–27 by Wilmott (*l.c.*) and Lacaita, and also by Lofthouse. These were advanced towards fruiting condition, but seeds were secured which gave rise to vigorous plants in culture. In 1929 appeared two specific descriptions based in great part on garden specimens. A slight difference in time of publication gives priority to the name *Lofthousei*.

Previous collections of plants from the Sierra Nevada akin to *P. elatior* have usually been referred to *P. intricata* (Pax, *l.c.*; Willk. et Lange, *l.c.*). That this Sierra Nevada plant comes near to *P. intricata* is the considered opinion of Wilmott (*l.c.*), who described it under *P. hispanica*. What data can be adduced to separate *Lofthousei* from that ally? Its robustness in contrast with *intricata* is generally commented on. But in its original Pyrenean localities *intricata* in its autumn stage tends to approximate in size. There is little or nothing in the shape of the leaves, in their

indentation or in the indumentum; the wing to the petiole may be narrowed or broad. The large size of the calyx (10–20 mm. long, usually 12–15 mm.) certainly exceeds what is usual in *intricata*, but in some species of *Primula* the calyx varies surprisingly in length. Of much greater significance is the small size of the limbs of the *infundibular* corolla, which is not flat. Collectors of the plant in the field who are familiar with *intricata*, and cultivators of both in conjunction in the garden, are agreed in regarding them as distinct. Additional evidence is supplied by the detailed crossing experiments carried out on *Lofthousei* by Professor Harrison, with whom we have had the advantage of discussing the problem involved. Harrison found it possible to effect crosses between it and *P. Juliae* and *P. vulgaris*. But ineffective were attempts to hybridise it with *P. elatior* or with subsp. *intricata*. It is his view, therefore, that *Lofthousei* stands as a specific unit well apart from the other *Vernales*. Our own tendency is to regard it as within the *elatior* complex.

P. elatior subsp. **Pallasii** (Lehm.) W. W. Sm. et Forrest in Notes Roy. Bot. Gard. Edin., xvi, 42 (1928), and in Journ. Roy. Hort. Soc., liv, 21 (1929). *P. Pallasii* Lehmann, Monog. Primul., 38, t. 3 (1817); Boiss. Fl. Orient., iv, 26 (1879)—excl. var. β ; Bot. Reg., t. 896 (1825); Lodd. Bot. Cab., xvi, t. 1585 (1829); Ruprecht in Bull. Acad. St. Pétersbourg, vi, 224 (1863); Journ. Roy. Hort. Soc., xxxix, 168, 171 (1913); Harrison in Trans. North. Nat. Union, i, 49, 56, 65, 74, 75 (1931). *P. elatior* var. *Pallasii* (Lehm.) Pax in Engl. Bot. Jahrb., x, 179 (1889); Journ. Roy. Hort. Soc., vii, 287 (1889); Korshinsky in Mém. Acad. Pétersbourg, Ser. 8, vii, 284 (1898); Sommier et Levier in Acta Hort. Petrop., xvi, 332 (1900)—*pro parte*; Kusnetzow, Fl. Cauc. Crit., iv, 58 (1901); Pax in Engl. Pflanzenr. Primulaceae, 51 (1905); Turkevicz, Fl. Ross. Asiat., i, 14 (1923); Busch in Fl. Sib. et Orient. Extr., iv, Cem. 65, 20, figs. pp. 22, 24 (1926). *P. elatior* var. *genuina* Trautvetter in Act. Hort. Petrop., v, 455 (1877). *P. altaica* Pall. ex Ledeb. Fl. Alt., i, 20 (1829).

The first diagnosis of this plant was based on specimens collected by Pallas in the Altai. From Lehmann's brief statement may be cited: Leaves obovate-oblong, glabrous, erose-dentate, decurrent into the petiole; umbel 3–6-flowered, pubescent. Lehmann supplied a figure, called "icon mala" by Pax (*l.c.*), but nevertheless a very fair representation of an Altai specimen at Edinburgh (ex

herb. *Fischer*)—almost certainly from the material of Pallas. Subsequent commentators have as a rule assessed Lehmann's species as no more than a variety. Thus Ruprecht (*l.c.*) thought it would prove to be a more glabrous variety of his *P. amoena* β *flava* (*i.e.* subsp. *Ruprechtii*). Pax (*l.c.*) subjoined it to *P. elatior*, and that view was accepted by Kusnetzow, by Turkevich and by Busch, all well acquainted with the Caucasian-Siberian flora. From the allies of its region it is readily separated by the glabrous decurrent leaf-blades. In facies it bears a strong resemblance to the European subsp. *intricata*, which has a fine pubescence on both sides of the leaf. Both plants show a transition from broad leaves fairly well indented to narrow leaves with feeble teeth or subentire.

Subsp. *Pallasii* has a distribution from the Urals and the Caucasus through Turkey (Anatolia) to Armenia, Persia, and the Altai. It is recorded from the European side of the Urals in the province of Perm. It was introduced into culture in this country in 1822 (Bot. Reg., *l.c.*). In Edinburgh it may flower as early as February.

P. elatior* subsp. *pseudoelatior (Kusnetzow) W. W. Sm. et Forrest in Notes Roy. Bot. Gard. Edin., xvi, 42 (1928), and in Journ. Roy. Hort. Soc., liv, 21 (1929). *P. pseudoelatior* Kusnetzow, in Act. Hort. Bot. Univ. Imp. Jurjev., i, 68 (1900), and in Fl. Cauc. Crit., iv, 63 (1901); Pax in Engl. Pflanzenr. Primulaceae, 49 (1905); Journ. Roy. Hort. Soc., xxxix, 168, 171 (1913); Grossheim, Fl. Kavkaza, iii, 206 (1932). *P. Pallasii* subsp. *pseudoelatior* (Kusnetzow) Harrison in Trans. North. Nat. Union, i, 49, 65, 74 (1931).

In his diagnosis Kusnetzow cites the following criteria: Leaves rugose abruptly contracted into the petiole, cordate at the base or subcordate or abruptly truncate, ovate, rather pale below and hairy, crenate; . . . calyx finely glandular-hairy, narrowly cylindrical, with broadly lanceolate teeth equalling the tube or a little shorter; . . . capsule rotundate, much shorter than the calyx.

To these points may be added that in our specimens (collected by Turkevich) the leaves are 4–5 cm. long, 3–4 cm. broad, grey- or whitish-tomentose below; petiole equalling or longer than the blade, unwinged or evenly winged throughout; calyx 1.2–1.5 cm. long, stout, cleft to one-third or almost one-half.

It is evident from the notes appended by Kusnetzow that material of this plant in Russian herbaria had previously been assessed as

P. amoena or *P. elatior* or varieties thereof. Pax (*l.c.*) had no specimens, and repeated the account of Kusnetzow from which he thought the plant better placed as a variety of *P. elatior*. It is a native of the Caucasus, occurring in Georgia, Abkhazia, and in the North. Its cordate tomentose leaves distinguish it from its allies in that region. Its general facies, its long calyx, and its rounded capsule (if that is confirmed in maturity) render it somewhat prominent among the subspecies. Kusnetzow's assessment of it as a species may be correct.

P. elatior subsp. **Ruprechtii** (Kusnetzow) Harrison in Trans. North Nat. Union, i, 49, 74, 76 (1931). *P. Ruprechtii* Kusnetzow, in Act. Hort. Bot. Univ. Imp. Jurjev., i, 68 (1900), and in Fl. Cauc. Crit., iv, 64 (1901); Journ. Roy. Hort. Soc., xxxix, 169, 171 (1913); Grossheim Fl. Kavkaza, iii, 206 (1932); Quart. Bull. Alp. Gard. Soc., ii, 297 (1934) *P. leucophylla* var. *Ruprechtii* (Kusnetzow) Pax in Engl. Pflanzenr. Primulaceae, 53, fig. 23A (1905); Engl. and Drude, Veget. Erde, x, II, 55 (1908). *P. leucophylla* subsp. *Ruprechtii* (Kusnetzow) W. W. Sm. et Forrest in Notes Roy. Bot. Gard. Edin., xvi, 42 (1928), and in Journ. Roy. Hort. Soc., liv, 21 (1929). *P. amoena* var. *flava* Ruprecht in Bull. Acad. St. Pétersbourg, vi, 223 (1863). *P. elatior* var. *amoena* Regel in Acta Hort. Petrop., iii, 133 (1874)—*pro parte*. *P. amoena* Boiss. Fl. Orient., iv, 26 (1879)—*pro parte*. *P. amoena* var. *genuina* Pax in Engl. Bot. Jahrb., x, 180 (1889)—*pro parte*.

The first mention of this plant was by Ruprecht (*l.c.*), who considered it a yellow-flowered form of *P. amoena*. Kusnetzow gave it specific status, and Pax transferred it as a variety to his *P. leucophylla*. For the difference between them, see under subsp. *leucophylla*. It is a native of the Caucasus and of Russian Armenia, growing at 1000–3000 m. Of its nearest of kin in the Caucasus, it is separated from subsp. *cordifolia* and subsp. *pseudoelatior* by the decurrent lamina, and from the subglabrous subsp. *Pallasii* by its dense tomentum.

HYBRIDS OF *P. ELATIOR* (L.) Hill.

P. elatior (L.) Hill × **P. vulgaris** Huds.; Grenier Fl. Chain. Jurass., 500 (1865–75); Lüdi in Hegi, Illust. Fl. Mittel-Eur., v, 1785 (1927); Harrison in Trans. North. Nat. Union, i, 75–76 (1931). *P. acaulis* × *P. elatior* Muret in Reuter, Catal. Pl. Genève, 144

(1861); Ljungström in Bot. Zentralbl., xxxv, 182 (1888); Beyer in Abh. Bot. Ver. Brandenburg, xxix, 26 (1888); Pax in Engl. Bot. Jahrb., x, 184 (1889); Widmer, Eur. Art. Prim., 132 (1891); Pax in Engl. Pflanzenr. Primulaceae, 61 (1905).

= × ***P. digenea*** Kerner in Österr. Bot. Zeitschr., xxv, 79 (1875); Beck, Fl. Niederösterr., 916 (1893); Pax, *l.c.*, 61; Lüdi in Hegi, *l.c.* *P. fallax* C. Richter, Exsicc. ex parte. *P. Falkneriana* Porta, Exsicc. ex parte.

A native of Great Britain, Belgium, France, Switzerland, Bavaria, Austria, etc., this hybrid is more or less intermediate between the parents. There is an obvious scape and the flowers are solitary, with none arising from the base. The pedicels are much longer than the calyx, and the limb of the corolla is from 2 cm. to 2.5 cm. in diameter.

There are other forms of this cross:

× ***P. ANISIACA*** Stapf in Sched. ad. Fl. Austr. Hung., iv, 45 (1886); Beck, *l.c.*, 914; Pax, *l.c.*

This form of the cross is nearer *P. vulgaris* than *P. elatior*. There is a short many-flowered scape and the pedicels are much longer than the calyx. A native of Belgium, Holstein, Switzerland, and Lower Austria.

× ***P. CAULESCENS*** Pax, *l.c.*, 61 (omitting all synonyms as these are doubtful and mainly referable to *P. vulgaris* var. *caulescens*. See p. 458. The origin of the hybrid might equally well have been *P. veris* × *P. vulgaris*. See Miller Christy in New Phyt., xxii, 233).

According to Pax a secondary hybrid which approaches *P. vulgaris* in its foliage and flowers. The leaves are longer, however, and there is an elongate scape. No basal flowers are present and the corolla is 2–3 cm. in diameter. It is a native of Germany, Austria, and Switzerland.

× ***P. FALKNERIANA*** Porta, Exsicc. 1882; Pax, *l.c.*, 62.

Another secondary hybrid, this time approaching *P. elatior*. The scape is longer than the leaves and there are no basal flowers. The flowers are frequently nodding, and are carried on pedicels as long as or longer than the calyx. The corolla is 18–22 mm. in diameter. Native of Germany, France, Austria, and elsewhere.

P. elatior form. **colorata** Pax $\times$ **P. vulgaris** Huds.; Lüdi in Hegi Illust. Fl. Mittel-Eur., v, 1785 (1927). *P. acaulis* $\times$ *P. elatior* var. *genuina* f. *hortensis* Pax in Engl. Pflanzenr. Primulaceae, 62 (1905).

= $\times$ **P. purpurascens** (Camus) Beck, Fl. Niederöstr., 914 (1893); Pospichal, Fl. Österr. Küstenlandes, ii, 456 (1899); Pax, *l.c.*, 62; Lüdi in Hegi, *l.c.* *P. acaulis* var. *purpurascens* Camus in Bull. Soc. Bot. France, xxxvii, 173 (1890).

A horticultural plant with dull-purple flowers about 2 cm. in diameter, carried on a short scape. Sometimes there are solitary basal flowers.

P. elatior (L.) Hill $\times$ **P. veris** L.; Lüdi in Hegi, Illust. Fl. Mittel-Eur., v, 1785 (1927); Harrison in Trans. North. Nat. Union, i, 75-76 (1931). *P. elatior* $\times$ *P. officinalis* Muret in Reuter, Catal. Pl. Genève, 143 (1861); Beyer in Abh. Bot. Ver. Brandenburg, xxix, 26 (1888); Ljungström in Bot. Centralbl., xxxv, 182 (1888); Pax in Engl. Bot. Jahrb., x, 184 (1889); Widmer, Eur. Art. Prim., 135 (1891); Beck, Fl. Niederöstr., 916 (1893); Pax in Engl. Pflanzenr. Primulaceae, 60 (1905).

= $\times$ **P. media** Petermann, Analyt. Pflanzenschlüssel, 364 (1846); Fl. Deutschl., 460 (1849); Kerner in Österr. Bot. Zeitschr., xxv, 80 (1875); Pax, *l.c.*, 60; Lüdi in Hegi, *l.c.* *P. unicolor* Nolte in Hans. Herb., No. 1159; Lange, Danske Fl., Ed. 3, 181 (1864); in Bot. Tidsskr., xiv, 152 (1884). *P. elatior* var. *decipiens* Sonder, Fl. Hamburg, 113 (1851). *P. lateriflora* Goupil in Mém. Soc. Linn. Paris, iii, 250, t. 10 (1825)? *P. Tommasinii* Lange in Fl. Dan., t. 2767 (1867). *P. glabrescens* Arv.-Touvet. Diagnos., 51 (1871)? ex Beck. *P. leudrensis* Porta, Exsicc.

A hybrid form from Holstein, through Germany to Bohemia and Savoy. It is more or less intermediate between the parents, differing from *P. elatior* in its shorter habit, inflated calyx, larger pale yellow, not bright yellow, corollas with flatter limb.

Other forms of this cross are:—

$\times$ **P. SILENIFLORA** H. Schmidt in 75. Jahresb. Schles. Ges., 13 (1898); in Deutsch. Bot. Monatschr., xviii, 58 (1900); Pax, *l.c.*, 61.

A Silesian plant with the corolla divided to the base.

- × **P. SORDIDA** Beck, Fl. Hernst. Kl. Ausg., 408; Fl. Niederösterr., 917 (1893); Pax, *l.c.*, 60.

Flowers dullish-purple. In culture as well as in the wild condition.

- P. elatior** (L.) Hill × **P. veris** subsp. **canescens** (Opiz) Hayek; Lüdi in Hegi, Illust. Fl. Mittel-Eur., v, 1785 (1927).

- = × **P. fallax** C. Richter in Abh. Zool. Bot. Ges. Wien, xxxvi, 194 (1887). Pax in Engl. Pflanzenr. Primulaceae, 61 (1905): Lüdi in Hegi, *l.c.*

A native of Northern Austria, with the under surface of the leaves thinly covered with a canescent tomentum.

- P. elatior** (L.) Hill × **P. veris** subsp. **Columnae** (Ten.) Lüdi in Hegi, Illust. Fl. Mittel-Eur., v, 1785 (1927).

- = × **P. brevifrons** Borbás in Természetr. Füzetek, 166 (1901); in Österr. Bot. Zeitschr., lii, 195 (1902); Pax in Engl. Pflanzenr. Primulaceae, 61 (1905); Lüdi in Hegi, *l.c.*

Another plant with the leaves canescent-tomentose below. Native of Hungary and Switzerland.

- P. elatior** (L.) Hill × **P. veris** subsp. **macrocalyx** (Bunge) Lüdi in Hegi, Illust. Fl. Mittel-Eur., v, 1753 (1927).

- = × **P. Goppertiana** Pax in Engl. Pflanzenr. Primulaceae, 61 (1905).

A plant with a campanulate calyx. Once cultivated in the Breslau Botanic Garden.

- P. Juliae** Kusnetzow in Acta Hort. Jurjev., i, 67 (1901) et Fl. Cauc. Crit., iv, 75 (1901); Pax in Engl. Pflanzenr. Primulaceae, 56 (1905); Irving in Gard. Chron., li, 293, with fig. (1912); Bot. Mag., t. 8468 (1912); Journ. Roy. Hort. Soc., xxxviii, fig. 40 on proc. p. lvii (1912); *ibid.*, xxxix, 168, 171–172 (1913); *ibid.*, xlii, proc. p. lx (1916); Jardin, xxvi, 215 (1912); The Garden, lxxviii, 193, fig. p. 194 (1914); *ibid.*, lxxx, 202, with fig. (1916); Mottet in Rev. Hort., 250, fig. 75 (1914); Gard. Chron., lxiii, 195, with fig. (1918); *ibid.*, lxiii, 225, with fig.

(1918); Farrer, Eng. Rock Gard., ii, 146, pl. 13 (1919); Journ. Roy. Hort. Soc., xlv, proc. p. lxxv (1919); *ibid.*, xlv, proc. p. xxxii (1919); *ibid.*, xlv, proc. p. xxxvii (1920); *ibid.*, xlviii, 62 (1923); Gard. Chron., lxxi, 145 (1922); *ibid.*, lxxii, 36 (1922); The Garden, lxxxvi, 118 (1922); *ibid.*, lxxxvii, 121 (1923); *ibid.*, lxxxviii, fig. p. 548 (1924); *ibid.*, xci, 54, with fig. (1927); Gard. Chron., lxxix, 397 (1926); Ingwersen in *ibid.*, lxxxiii, 152 (1928); W. W. Sm. & Forrest in Notes Roy. Bot. Gard. Edin., xvi, 42 (1928), and in Journ. Roy. Hort. Soc., liv, 11, 21, fig. 12 (1929); Gould, *ibid.*, liv, 75 (1929); Huskins, *ibid.*, liv, 95–100 (1929); Chittenden in Journ. Genetics, xix, 286–291, 312–314, pl. 21 (1928); Harrison in Trans. North. Nat. Union., i, 48, 59, 62, 65–66 (1931); Bruun, Cytological Studies in Primula, 36, 41 (1932); Grossheim, Flora Kavkaza, i, 3, 206 (1932); Journ. Roy. Hort. Soc., lix, proc. p. xxiv (1934); *ibid.*, lx, proc. p. lxx (1935); Quart. Bull. Alp. Gard. Soc., iii, 166 (1935).

This very attractive species was discovered in April 1900 by Madame Julia Ludovikovna Mlokossjewicz near Lagodechy in Kachetia, some 80 miles E.N.E. of Tiflis, province of Georgia in the Caucasus. According to Grossheim (*l.c.*) it has not been recorded outwith Georgia. In his diagnosis Kusnetzow lays emphasis on the glabrous reniform-orbiculate cordate leaves with long distinct petioles, on the numerous one-flowered scapes and on the narrowly tubular calyx. It was assigned without any doubt to the Paxian section Vernales. For his Monograph Pax (*l.c.*) unfortunately had no material and his statement is based on that of Kusnetzow. The introduction of *P. Juliae* into cultivation followed soon after its discovery. It flowered at Dorpat with Kusnetzow, who forwarded plants in 1911–12 to Oxford and to Kew. It was figured forthwith in the Botanical Magazine (*l.c.*), where it is remarked that the flower-stalks scarcely, if at all, exceed the leaves, whereas Kusnetzow describes them as two to three times as long. Specimens in the Edinburgh Herbarium, collected by the original finder, show that the species is variable in this respect and both statements are correct. Living plants were received in Edinburgh in 1912 by Balfour, who left a note (in herb.) to the effect that it is “allied to *P. megaseaefolia*, with which it forms a distinct group in its section and from which its habit, smaller crenate leaves and solitary axillary flowers separate it”. Later, however (Journ. Roy. Hort. Soc., xxxix, 174 (1913)), he relegated *P. megaseaefolia* to a section of its own.

Confirmation of the place of *P. Juliae* in the Vernales section is almost superfluous, but the cytological investigations of Chittenden (*l.c.*), Harrison (*l.c.*), and Bruun (*l.c.*) are in agreement and in full support, as is also the facility with which it hybridises with various members of the section. That its nearest of kin is *P. megaseaeifolia* is more doubtful, for the apparent approximation in leaf-shape is not a criterion of moment. Whether it hybridises with *P. megaseaeifolia* is a problem which so far does not appear to have been carried out successfully.

A small stoloniferous efarinose perennial with a long thin rhizome. Leaves forming a rather loose rosette, 2–8 cm. long, including the petiole, in cultivated specimens up to 10 cm. long; lamina 0.5–3 cm. long and broad, reniform-orbiculate to ovate-orbiculate, deeply cordate at the base, coarsely crenate at the margin, thin in texture, glabrous and efarinose on both surfaces; mid-rib and 4–5 pairs of lateral nerves impressed above, prominent below; petiole usually 2–3 times as long as the lamina, sometimes subequal to the lamina, slightly winged and sheathing at the base, glabrous, streaked with red. Scape obsolete; pedicels numerous, as long as, or 2–3 times longer than, the leaves, glabrous, streaked with red. Calyx 5–8 mm. long, narrowly tubular, markedly 5-angled, glabrous, cut to the middle or almost so into narrowly lanceolate acuminate very minutely ciliolate lobes. Corolla exannulate, heteromorphic, rose, with a yellowish tube and yellow and dark red eye; tube twice the length of calyx or even a little longer, very narrowly cylindrical, ampliate above insertion of stamens; limb 2–3 cm. in diameter with obcordate deeply emarginate lobes which are sometimes irregularly erose. Stamens, with anthers 1.5 mm. long, inserted in middle of corolla-tube in pin-eyed flowers and at apex in thrum-eyed. Long style as long as corolla-tube; short style half as long. Capsule . . . Seeds . . .

P. Juliae is hardy in culture and has a long flowering season from spring almost into winter. But its position in gardens has been quite overshadowed by the number of fine hybrids in which it is concerned. These are now extensively grown, and van Dijk in Journ. Roy. Hort. Soc., lxxi, 69 (1946), notes that they are now so popular that, in Holland at least, they occupy the first rank among garden Primulas. The wide range of crosses which can be carried out within the Vernales with *P. Juliae* as one of the parents is well indicated by the experiments carried out by Harrison (*l.c.*, 75). Some of the hybrids of distinct horticultural merit raised in this country are given a review by Ingwersen (*l.c.*). These have a long

period of blossoming, as has *P. Juliae* itself, are usually fertile but do not breed true. Among those which have attained more than a brief prominence may be mentioned: Ansoldii, Condor, Crispai, Dark Juliae, Dorothy, Eastern Queen, Hellenae, Icombe var., The Jewel, Juliana var. alba, Juliana var. Gloria, Lilac Juliae, Lilac Time, Lingwood Beauty, Lord Lascelles, Merton Hybrid, Mrs. McGillivray, Nacre, Old Rose, Profusion, Purple King, Purple Splendour, Sulphur Juliae, Tinker Bell, Violetta, Wanda, White Rose, White Wanda.

P. megaseaeifolia Boiss. Fl. Orient., iv, 26 (1879); Pax in Engl. Bot. Jahrb., x, 170 (1889); Gard. Chron., xxix, 222, fig. 84 (1901); Journ. Roy. Hort. Soc., xxvi, proc. p. lxix, fig. 133 (1901); Fomin in Acta Hort. Bot. Univ. Jurjev., ii, 63 (1901); Kusnetzow, Fl. Cauc. Crit., iv, 57 (1902); Bot. Mag., t. 7901 (1903); Flora and Sylva, ii, 24 (1904); The Garden, lxxv, 323 (1904); Pax in Engl. Pflanzenr. Primulaceae, 46 (1905); Möllers Deutsche Gärtn.-Zeit., xxi, 2 (1906); Mottet, Monogr. Genre Primevère, t. 4 (1912); Balf. f. in Journ. Roy. Hort. Soc., xxxix, 147, 168, 174, 219, fig. 83 (1913); Hill in Journ. Genetics, ii, 14 (1913); Farrer, Engl. Rock Gard., ii, 156 (1919); W. W. Sm. and Forrest, Notes Roy. Bot. Gard. Edin., xvi, 27 (1928), and in Journ. Roy. Hort. Soc., liv, 20, fig. 61 (1929); Gard. Chron., lxxxvii, 187, fig. 74 (1930); Bruun, Cytological Studies in Primula, in Symb. Bot. Upsal., i, 35, 36, 125 (1932); Grossheim in Fl. Kavkaza, i, 3, 205 (1932). *P. megaseaeifolia* forma *superba* Gard. Chron., xxxv, 267 (1904); Pax *l.c.*, 47.

This very distinct species was discovered by Balansa, an eminent collector, in May 1866, near Rhizé in Lazistan, a town 40 miles east of Trebizond. It was growing in moist shady defiles at an elevation of 300 m. For a long time the plant was believed to be restricted to this one locality (Bot. Mag., *l.c.*), and in any case gatherings in the field have been very occasional. Fomin (*l.c.*) records in 1901 that on a journey completed in the beginning of February in the Batum province in the neighbourhood of Chakva he secured this rare species which, he states, always flowers at that time of year. At one time it was fairly abundant, growing among Rhododendrons, almost on the very shores of the sea, on slopes along the railway. Owing to the uprooting of the overgrowth of Rhododendrons, the Primula had almost disappeared. Balls (*in herb.*) reports finding the species at 660 m. in the Trebizond province growing on moss and on non-limestone rock under dense shrubs. Grossheim (*l.c.*) limits

its occurrence in the Caucasus to Georgia. (The statement in "The Garden" (*l.c.*), indicating wide distribution in the Caucasus, Persia, and Afghanistan, is not supported by any evidence.)

Its position in the genus has been very variously assessed. Boissier (*l.c.*) compared the corolla in size to that of *P. amoena*, but his placing of the species in proximity to *P. grandis* cannot be interpreted that in his view they were akin. Pax (*l.c.*) in his first analysis of the genus in 1889 associated *P. megaseaefolia* with three Japanese species with cordate leaves. In his Monograph Pax (*l.c.*, 46) went still further afield for his comparison and ascribed the plant to his section *Carolinella*, an association for many reasons inadmissible. Balfour (*l.c.*, 174) regarded it as an isolated member of the genus and proposed for it a separate section. In this he was followed by Smith and Forrest, who suggested, however, that it tended towards *P. Juliae* and therefore towards section *Vernales*. This opinion was fully confirmed by the cytological analysis of Bruun (*l.c.*). "Vernales and *Megaseaefolia* constitute a separate branch of the genus, so far removed from other sections that no kinship with any other group can be demonstrated cytologically." The work of Bruun, as well as the geographical distribution, favours its inclusion within the *Vernales*, and not far away from *P. Juliae*.

Its introduction into European cultivation is credited by Pax (*l.c.*) to Dammann & Co. in 1896. It was brought to this country in 1901 by Miss Willmott. A large-flowered form, perhaps no longer extant, was in culture in 1904 (*Gard. Chron.*, *l.c.*). It is a hardy species, but as it flowers in the winter months it is not happy out of doors. It is comparatively rare in gardens, and this may be due to its reluctance to produce ripe capsules.

There is no satisfactory evidence that *P. megaseaefolia* has been effectively used in hybridisation experiments. But for some time it was accepted that Herr Arends of Ronsdorf had crossed *P. obconica* with *P. megaseaefolia* as the male parent. Pax, then engaged on his Monograph, had his attention directed to this presumed hybrid and decided that it showed definite intermediate characters. He therefore described it under the name *P. Arendsii* (Pax, *l.c.*, 346). In 1905 it was shown to the Royal Horticultural Society and obtained an Award of Merit (*Journ. Roy. Hort. Soc.*, xxxi, p. cxxx (1906)). It continued in culture for some years as *P. obconica gigantea* (*Journ. Roy. Hort. Soc.*, xxxv. 558 (1909); *Gartenf.*, lvii, 632 (1908)). An analysis, however, was made by Hill (*Journ. Genetics*, ii, 14 (1912)), who decided that "the plants do not appear to show any character which can be definitely attributed to

the influence of the pollen of *P. megaseaeifolia*". The observations of Bruun (*l.c.*) on the cytology of *P. megaseaeifolia* are conclusively in favour of Hill's verdict.

A hairy perennial with a long fairly stout rhizome producing numerous fleshy roots and surmounted by many ovate to lanceolate, acuminate purplish scale-leaves 5–15 mm. long. Leaves, including the petiole, 3·5–20 cm. long; lamina 2·5–15 cm. long, 2·5–12 cm. broad, ovate to ovate-rotundate or orbicular, rounded at the apex, usually cordate but sometimes subrotundate at the base, sub-spinulosely crenate-dentate to subentire at the margin, chartaceous in texture, dark green and glabrous above, paler below and tawny-pubescent along the nerves; veins sunk in the upper surface; mid-rib and 5–7 pairs of lateral nerves conspicuous below; reticulation rather wide and more or less obscure; petiole 1–10 cm. long, tinged with red, markedly vaginate at the base, covered with long tawny septate hairs. Scape 5–15 cm. long, stout, reddish-tinted, pilose or glabrescent, carrying a terminal umbel of 3–9 flowers or two superposed umbels; bracts 5–10 mm. long, lanceolate, acuminate at the apex, minutely puberulous; pedicels 1–2·5 cm. long, stout, faintly puberulous, more or less erect or semi-pendent. Calyx 10–15 mm. long, tubular, markedly 5-keeled, cut to a third into lanceolate, acuminate teeth. Corolla rose, changing to bluish-rose, with a small whitish-yellow eye, exannulate, heteromorphic: tube slightly longer than the calyx, cylindrical, ampliate above insertion of stamens; limb 1·5–2·5 cm. in diameter, with obcordate deeply emarginate lobes. Stamens, with anthers about 2 mm. long, inserted near apex of corolla-tube in thrum-eyed flowers, near middle of tube in pin-eyed. Long style as long as corolla-tube or slightly exserted; short style half the length of corolla-tube. Capsule a little longer than the calyx, oblong, dehiscing by 10 longitudinal teeth. Seeds (ex Boissier) angular-spherical, tuberculate.

P. veris Linn., Sp. Pl., i, 142 (1753); Huds., Fl. Angl., 70 (1762); Huds., *ibid.*, i, 84 (1778); Kniphof, Herb. Viv., ii, t. 878, 880, 882 (1762); Hill, Herb. Brit., ii, t. 128 (1770); Zorn, Ic. Pl. Med., i, t. 7 (1779); Bergeret, Phyt. Univ., i, 61 (1783); Hoppe, Ect. Pl. Ratisb., t. 141 (1788); Batsch, Anal. Fl., i, t. 4, fig. 6a–6h (1790); Sowerby and Sm., Eng. Bot., i, t. 5 (1790); Baylis, Bot. Phys., t. 46 (1791); Oskamp, Afb. Artseny-Gewass., i, t. 7 (1796); Svensk Bot., i, t. 5 (1802); Mirbel, Hist. Nat. Pl., xiv, t. 96 (1802–06); McDonald, Dict. Pract. Gard., ii, t. 40

(1807); Roques, Pl. Usuell. Indig. and Exot., ii, t. 18 (1808); Thornton, Brit. Flor., ii, 66 (1812); Vigneux, Pl. Pitt. Envir. Paris, t. 12 (1812); S. Edwards, New Bot. Gard., ii, t. 40 (1812); Hayne, Getreue Darst. Arzn. Gewächse, iii, t. 34 (1813); Dict. Sc. Nat., Planch. Bot. Dicot., t. 25 (1816-29); Chaumeton, Fl. Méd., v, t. 284 (1818); Curtis, Fl. Londin., Ed. 2, iii, fasc. vi, t. 15 (1826); Nees, Pl. Offic., i, t. 152 (1828); Baxter, Brit. Bot., Ed. 2, ii, t. 89 (1835); Zenker, Fl. Thüringen, i, t. 15 (1836-55); Dietrich, Fl. Boruss., vi, t. 403 (1838); Maund, Bot. Gard., xi, t. 253 (1839-51); Jackson, Pict. Fl., fig. 307 (1840); Deakin, Florigr. Brit., i, fig. 324 (1841); Burnett, Pl. Util., i, t. 20a (1842); Loudon, Brit. Wild Fl., Ed. 2, t. 46 (1846); Duchesne, Pl. Util., t. 46 (1846); Cassone, Fl. Med.-Farm., v, t. 443 (1850); Johnson and Sowerby, Brit. Wild Fl., fig. 992 (1858-60); Johnson and Sowerby, Useful Pl. Gr. Brit., t. 15, fig. 179 (1861-62); Hogg and Johnson, Wild Fl. Gr. Brit., i, t. 54 (1863); Bentham, Handb. Brit. Fl., fig. 643 (1865); Réveil, Règne Vég., iii, t. 26; iv, t. 5; xiv, t. 9 (1870); Pratt, Fl. Pl., Grasses, Sedges and Ferns Gr. Brit., Ed. 3, iv, t. 168 (1873); Journ. Hort., lxiii, 497 (1880); Karsten, Deutsche Fl. Pharm.-medic. Bot., 910 (1880-83); Hoffmann, Pflanzen-atlas, t. 16, fig. 94 (1881); Journ. Roy. Hort. Soc., vii, 216, 287, 291, 292 (1889); Karsten, Fl. Deutschl., ii, 480 (1895); Miller Christy in Journ. Linn. Soc., xxxiii, 172 (1897); Journ. Roy. Hort. Soc., xx, proc. pp. xxxvi, xxxix (1896-97); *ibid.*, xxviii, 697 (1903-4); Step, Wayside and Woodl. Bloss., t. 2 (1895); C. T. Green, Fl. Liverpool Dist., fig. 404 (1902); Kirby, Brit. Fl. Pl., t. 76 (1906); Fitzgerald in Nature Book, ii, 284 (1909); Benth. and Hook. Handb. Brit. Fl., Ed. vi, 289 (1912); Journ. Roy. Hort. Soc., xxxix, 226 (1913); Perrin and Boulger, Brit. Fl. Pl., iii, t. 207, 214A, figs. 1-5 (1914); Bailey, Stand. Cycl. Hort., 2798 (1916); Lindman, Bild. Nord. Fl., t. 136 (1917-20); Fitch and Smith, Ill. Brit. Fl., Ed. rev. 4, Iss. 2, fig. 651 (1919); Bot. Exch. Cl. Report, 296 (1921); Babington, Man. Brit. Bot., Ed. 10, 341 (1922); Lüdi in Hegi, Ill. Fl. Mittel.-Eur., v, t. 208, pp. 1750, 1752 (1927); W. W. Sm. and Forrest, Notes Roy. Bot. Gard. Edin., xvi, 42 (1929), and in Journ. Roy. Hort. Soc., liv, 21 (1929); M. E. Eaton in Addisonia xvi, t. 517 (1931); Harrison in Trans. North. Nat. Union, i, 49, 52, 54-56, 61, 64, 66, 68-76 (1931); Javorky and Csapody, Ic. Fl. Hungar., 390 (1932); Stirling in Publ. Hart. Bot. Lab. Liverpool, No. 8 (1932); Bot. Exch. Cl. Report, 226 (1936).

P. officinalis (L.) Hill, Veg. Syst., viii, 25 (1765); Fl. Dan., iii, t. 433 (1769)—*vide* Lange, Nomencl. Fl. Dan., 14 (1887); Jacq. Misc. Austr., i, 159 (1778); Lamarek, Ill., i, t. 98, figs. 1 and 2 (1791); Schmidt, Fl. Boem., ii, 41, t. 165 (1793); Curtis, Fl. Londin., ii, fasc. vi, t. 16 (1798); Dreves & Hayne, Choix de Pl., t. 11 (1802); Sturm, Deutsch. Fl., iv, xiv (t. 212) (1803); A. & F. Plée, Herbor. Paris, t. 23 (1811); Schrank, Fl. Monac., iii, t. 266 (1816); Vietz, Ic. Pl. Med.-oec.-techn., ix, t. 764 (1819); Sterler, Eur. Med. Fl., t. 6 (1820); Koch, Synops. Fl. Germ., Ed. 1, 586 (1837); Plée, Types chq. Famille Pl. France, t. 123 (1844-64); Ledeb. Fl. Ross., iii, 8 (1847-49); Duby in DC. Prodr., viii, 36 (1844); Lorek, Fl. Pruss., Ed. 3, t. 49 (1848); Godr. et Gren. Fl. France, ii, 448 (1852); Reichb. Ic. Fl. Germ., xviii, t. 1090, 1106 (1855); Blytt, Norges Fl., i, 823 (1861); Argenta, Album Fl. Med.-Farm., ii, t. 196 (1863); Migout, Fl. Dépt. Allier, t. 13 (1866); Fuss, Fl. Transsylvan., 535 (1866)—*pro parte*; Schur, Enum. Pl. Transsylv., 553 (1866)—*pro parte*; Syme, Engl. Bot., vii, t. 1130 (1867); Cusin, Herb. Fl. Franç., xv, t. 4 (1874); Boiss. Fl. Orient., iv, 24 (1879); Wagner, Ill. Deutsche Fl., Ed. 2, 502 (1882); Schlechtendal, Lang. & Schenk, Fl. Deutschl., Ed. 5, t. 1968 (1884); Baillon, Ic. Fl. Franç., ii, t. 182 (1885-94); Simonkai, Enum. Fl. Transsylv., 459 (1886)—*pro parte*; Pax in Engl. Bot. Jahrb., x, 181 (1889); Caruel in Parlatore, Fl. Italian., viii, 615 (1889); Thomé, Fl. Deutschl., iv, t. 472 (1889); Journ. Roy. Hort. Soc., vii, 168, 234, 251, 268-269, 274, 276-279, 281-288, 290-291 (1889); Sagorski and Schneider, Fl. Centralkarp., 381 (1891), Widmer, Europ. Art. Prim., 128 (1891); Beck, Fl. Niederösterr., 915 (1893); Aclouque, Fl. France, 449 (1894); Garcke, Ill. Fl. Deutschl., 498 (1895); The Garden, i, 395 (1896); Reichenau, Mainzer Flora, fig. 30 (1900); Journ. Roy. Hort. Soc., xxv, 30 (1900-1); Sturm, Fl. Deutschl., Ed. 2, ix, t. 62 (1901); Fiori & Paol. Ic. Fl. Ital., 313 (1901); Bailey, Cycl. Amer. Hort., 1434 (1901); Lindman, Bild. Nord. Fl., t. 136 (1901-5); Coste, Fl. France, ii, 522 (1903); Bailey in Journ. Bot., xli, 145 (1903); Blytt, Haandb. Norg. Fl., Ed. Dahl., 567 (1906); Lazaro, Comp. Fl. Españ., ii, 597 (1907); Beih. Bot. Centralbl., xxiii, II, 23, t. 3 (1908); *ibid.*, xxvi, ii, 269 (1910); Heukels, Fl. Nederl., iii, 37, 38 (1909); Gartenwelt, xiii, 74 (1909); *ibid.*, xv, 270 (1911); Fedtschenko & Fler. Fl. Eur. Russia, 732 (1910); Journ. Roy. Hort. Soc., xxxix, 100, 168-169, 171, 223, 225 (1913); MacWatt, Primulas of Europe, 48-49 (1923);

Farrer, Engl. Rock Gard., ii, 163 (1928). *P. veris* var. *officinalis* Linn. Spec. Pl., Ed. 1, i, 142 (1753). *P. odorata* Gilib. Fl. Lithuan., i, 32 (1871); Stokes, Bot. Mat. Med., i, 291 (1812). *P. coronaria* Salisb. Prodr. Stirp. Chapel Allert., 117 (1796). *P. domestica* Hoffmannsegg, Verzeichnis. 2 and 3, Nachtr. 185 (1826)? *P. pistillaris* Hoffmannsegg (l.c.). *P. montana* Reuter ex Nyman, Consp. Fl. Eur., 603 (1878-82). *P. veris* Oeder, Fl. Dan., t. 434 (1770); Lehmann, Monogr. Primul., 27 (1817). *P. officinalis* var. *genuina* Pax in Engl. Bot. Jahrb., x, 181 (1889); Korshinsky in Mém. Acad. St. Pétersbourg, vii, 283 (1898); Pax in Engl. Pflanzenr. Primulaceae, 57 (1905). *P. officinalis* var. *micrantha* Caruel in Parlatore, Fl. Italian., viii, 615 (1889)? *P. officinalis* var. *genuina* form. *typica* Pax in Engl. Pflanzenr. Primulaceae, 57 (1905). *P. veris* subsp. *genuina* (Pax) Lüdi in Hegi, Illust. Fl. Mittel.-Eur., v, 1751 (1927).

A hairy perennial with a stout long or short rhizome girt at the apex with more or less fleshy scales formed by the bases of withered leaves; furnished with numerous fibrous roots. Leaves, including the petiole, 5-20 cm. long, 2-6 cm. broad at flowering time, enlarging at fruiting time, ovate to ovate-oblong, round or obtuse at the apex, abruptly attenuate at the base into the petiole, crenate to irregularly erose-crenate at the margin, rugose with the veins impressed above and prominent below, pubescent or glabrescent on the upper surface, thinly greyish or whitish-tomentose to glabrescent on the lower surface; petiole at first shorter than the lamina, later subequal, membranously winged, sheathing at the base. Scape 10-30 cm. tall, markedly pilose, carrying usually a many-flowered more or less secund umbel; bracts 2-7 mm. long, linear-lanceolate, acute, pilose; pedicels 3-20 mm. long, pilose, more or less drooping. Calyx 8-15 mm. long, tubular-campanulate, markedly 5-angled, pilose especially along the 5 angles, cut for a third into triangular acute sometimes mucronate lobes. Corolla bright yellow, with an orange mark at the base of the petals, exannulate, heteromorphic; tube more or less equalling the calyx, a ampliate above insertion of stamens; limb 8-15 mm. diameter, concave, with obcordate emarginate lobes. Stamens, with anthers 2 mm. long, inserted at apex of corolla-tube in thrum-eyed flowers, at middle of tube in pin-eyed. Long style equalling corolla-tube, short style half as long. Capsule ovate, longer than the calyx, dehiscing by apical teeth. Seeds 1-1.5 mm. or slightly more in diameter, ovoid or subspherical, or again irregularly cuboid, blackish, finely vesicular-surfaced.

P. veris is the most widespread species of the section, and as regards extent of territory is not surpassed by *P. farinosa* itself. It is found throughout Europe except the extreme north, and across the Urals and the Caucasus through Persia and Turkestan to the upper valley of the Amur. Over this vast area it has developed a wealth of variations which have been assessed by authors as species, subspecies, varieties and forms. These variations, whatever their status, are not always restricted by geographical limits, for some may occur in the same region yielding intraspecific hybrids and thus many intermediates. In many districts contact is frequently possible with the allied *P. vulgaris* and *P. elatior* and numerous interspecific hybrids have been recorded. In its manifestations *P. veris* has been subject to many conditions of climate, and its altitudinal range extends from sea-level to 2200 m. A factor of some importance is the long period of time during which the plant has been known to mankind. The name it now carries dates long before Linnaeus and even before Mattioli. Some centuries earlier, in the Middle Ages, the name was applied to more than one early-spring flower, not necessarily a *Primula*. Apart from popular and local names, other Latin terms were given to our plant, such as *herba paralysis*, *Verbasculum odoratum*, *Betonica alba*, but with Mattioli the name we now use was restricted to it. During the two centuries after Linnaeus *P. veris* has received the attention of botanists in every country of Europe. It possesses therefore a most extensive literature. Its many deviations from a presumed normal have been studied in detail. The majority of these have been very adequately summarised in the monographical publications of Pax (*l.c.*). But many names occur in local floras and in occasional papers which are not easy to assemble in a general statement nor justifiable to relegate to the silence of synonymy. (This is particularly true of minor variations which may or may not have their equivalents in more than one country. The problems therein involved demand cultural and genetic studies for their solution if haply these suffice.)

We have seen no reason to deviate in any great measure from the general framework instituted by Pax, making allowance for what has accrued during the forty years since his Monograph. Pax divided the species into four varieties—*genuina*, *macrocalyx*, *canescens*, and *Columnae*. It is preferable to regard these as subspecies, as is the view of Lüdi (*l.c.*). The first of these corresponds to the plant seen at Upsala and described by Linnaeus himself, and so can be assessed as the standard without need of a trinomial. To the three sub-

species fall to be added subsp. *Velenovskyi* and possibly subsp. *legionensis*, the latter a Spanish plant as yet imperfectly known. Of these six categories, the Linnaean and the three annotated by Pax are much the most important and it is expedient to deal with them first. Although there is good reason to discriminate between them, the criteria available tend to overlap and do not lend themselves to the structure of a simple key. The morphological data require to be supplemented by the geographical distribution which, however, is not always exclusive. The minor variations of each category will be dealt with later. The first task is to contrast what may be termed the typical plant and its three major subspecies. To this end full use has been made of the annotations of Pax (*l.c.*) and the detailed analysis of Lüdi (*l.c.*). (But in the circumstances a wide interpretation must be allowed to this summation of their work.)

P. veris: Lamina of the typical plant generally abruptly contracted at base with petiole well winged, weakly hairy to glabrescent; hairs $\frac{1}{6}$ – $\frac{1}{3}$ mm. long, stiff, unbranched, often capitate-glandular; calyx 8–15 mm., $\pm$ narrowly campanulate, not widely divergent at apex; corolla-tube usually exceeding calyx, limb concave, 9–12 mm. across. Common through the middle of Europe from Britain to the Urals, Sweden, Switzerland, and the Julian Alps; does not extend south beyond the Alps.

P. veris subsp. *canescens*: Lamina as a rule gradually decurrent into the winged petiole, grey-tomentose below; hairs $\frac{1}{2}$ – $\frac{3}{4}$ mm., tortuous and often branched and interwoven; calyx 16–20 mm., $\pm$ campanulate; corolla-tube as a rule scarcely exerted from calyx, limb 8–20 mm. across, flatter than in type. Danube valley, Silesia, Yugoslavia, S. Tyrol, Württemberg, Baden, W. Alps, S. France, N. Spain.

P. veris subsp. *Columnae*: Lamina of thick texture, more oval than elongate, generally cordate with petiole little if at all winged, thickly white-hairy below; hairs 1 mm. long, twisted, often branched, thickly interwoven; calyx 16–20 mm., campanulate, widened at apex, usually very hairy; corolla-tube exceeding calyx, limb 10–22 mm. across, with almost flat limb. Pyrenees, W. Alps, S. Switzerland, Apennines, Balkans, Greece, Pontus in Asia Minor, rarely in Middle Europe.

P. veris subsp. *macrocalyx*: Lamina generally narrowed to a long and winged petiole, more or less grey-tomentose to glabrescent below; hairs $\frac{1}{3}$ – $\frac{1}{2}$ mm. long, generally straight but flaccid, unbranched, too short to be interwoven, often with small glandular tip; calyx 15–20 mm., somewhat conical, divergent at apex, often very hairy, with short triangular lobes usually with a very pronounced apiculus; corolla-tube exceeding calyx, limb 18–28 mm. across. Turkestan, Soongaria, N. Persia, Caucasus, Urals, Crimea, Mid-Russia, Bohemia. Also according to Kusnetzow in the Siberian Altai.

MINOR VARIATIONS OF *P. VERIS*.

This list of minor divergences is not complete. Many more may lie hidden in local floras which are not accessible to us. Moreover, in many cases analysis has been carried to an extreme and no advantage is to be gained from the varietal titles applied to long and short styles in dimorphic species, to a calyx longer or shorter than usual, to a broader or narrower corolla-tube, etc. The same plethora of terms—in most cases for minutiae—is attached to *P. elatior* and to *P. vulgaris*. That some of the terms may be only synonymous is probable but there can be no certainty. For those who may wish to add to the list annexed the following references will be found serviceable: Goupil in Ann. Soc. Linn. Paris, iii, 237 (1825); Petermann, Fl. Lips. Excurs., 170 (1838); Opiz, Fl. Böhmens, ii, 195 (1839); Ljungström in Botaniska Notiser, 123 (1885), and in Botan. Centralbl., xxxv, 181 (1888); Beauverd in Bull. Soc. Bot. Genève, ix, 362 (1917); Domin in Act. Bot. Bohem., x, 174 (1931), and in Sched. Fl. Cechoslav. Exsicc., 174 (1931).

var. **alba** Harrison in Trans. North. Nat. Union, i, 54 (1931).

A plant with white flowers which has been recorded from Wales. This may be only the equivalent of forma *albiflora* q.v.

form. **albiflora** (Evers) Lüdi in Hegi, Illust. Fl. Mittel.-Eur., v, 1751 (1927).

A form with white flowers reported from Trient in S.W. Switzerland.

var. **ampliata** (Koch) Lüdi in Hegi, *l.c.*; Harrison, *l.c.* *P. officinalis* var. *ampliata* Koch, Synops. Fl. Germ., Ed. 1, 587 (1837); R. Beyer in Abh. Bot. Ver. Brandenburg, xxx, 323 (1888); Pax in

Engl. Pflanzenr. Primulaceae, 57 (1905). *P. veris* subsp. *minoriflora* var. *genuina* f. *ampliata* Domin in Act. Bot. Bohem., x, 175 (1931).

Found occasionally with the normal plant, particularly in the eastern part of the latter's territory. It is distinguished by the broadly campanulate calyx widely open at apex.

var. **ascapa** (Goiran) Lüdi in Hegi, *l.c.*, 1752. *P. officinalis* var. *ascapa* Goiran ex Caruel in Parlatore, Fl. Ital., viii, 615 (1889). *P. officinalis* f. *ascapa* (Goiran) Pax, *l.c.*, 58. *P. veris* subsp. *minoriflora* var. *genuina* f. *ascapa* Domin, *l.c.*

A plant with obsolete scape and very short pedicels. First recorded from near Verona in N. Italy. Lüdi (*l.c.*) refers to experiments carried out by Dahlgren which show that the scapeless character can be transmitted.

form. **autumnalis** Lüdi in Hegi, *l.c.*, 1751. *P. officinalis* form. *autumnalis* Pax, *l.c.* *P. veris* subsp. *minoriflora* var. *genuina* f. *autumnalis* Domin, *l.c.*

This is regarded as an autumn form of the typical plant with a sparse-flowered umbel of smaller flowers. Pax cites England for its occurrence.

var. **biumbellata** Goupil in Ann. Soc. Linn. Paris, iii, 252 (1825); Harrison, *l.c.*

A plant with two superposed umbels. This circumstance occurs fortuitously in various species of *Primula* which have normally only a single umbel. The name is unnecessary but has been given.

form. **calycida** (Schube) Lüdi in Hegi, *l.c.* *P. officinalis* f. *calycida* Schube in 81 Jahresb. Schles. Gesellsch., 60 (1904); Pax, *l.c.*

In this form the calyx is cleft to the base. An abnormality reported from Silesia.

form. **hortensis** (Pax) Lüdi in Hegi, *l.c.* *P. officinalis* f. *hortensis* Pax, *l.c.*, 57. *P. officinalis* var. *rubrofusca* Lamotte, Fl. Plat. Centr. France, 514 (1881)? *P. veris* subsp. *hortensis* Domin, *l.c.*

A garden form with red flowers and a calyx 2 cm. long. It occurs as an escape in N. Germany according to Pax and Lüdi and no doubt elsewhere.

form. **horticola** (Domin) Lüdi in Hegi, *l.c.*, 1753. *P. horticola* Domin in Beih. Bot. Centralb., xxiii, 2 Abt., 23, fig. 2 (1908), and

ibid., xxvi, 2 Abt., 269, fig. 4b (1910), and in Act. Bot. Bohem., x, 175 (1931).

Domin gives a very complete account of this peculiar plant which was found in the Botanic Garden of the University of Praha. It is only half the size of the normal *P. veris* and the flowers are diminutive only 16–19 mm. long and 7–8 mm. across. Lüdi calls it a mutation. Domin describes it first as a species and later as a subspecies.

var. **longifolia** Lüdi in Hegi, *l.c.*, 1752.

Lamina small, gradually narrowed into a long much-winged petiole; calyx 15 mm., fairly narrow. Valais and Vaud in Switzerland. Numerous transitions between it and subsp. *Columnae* var. *valesiaca* (q.v.).

var. **obscura** Harrison, *l.c.*

A form differing only in the darker colour of the foliage. It is comparable to what is found in *P. vulgaris* var. *obscura* (q.v.). It is reported in Britain from Northumberland and Durham (Harrison in litt.).

var. **pallescent** Harrison, *l.c.*, 53.

Flowers a pale cream. Recorded from Northumberland and Durham; common on sand dunes at Hart, scarce on the railway cuttings near Birtley. Presumably not quite synonymous with *f. pallida* (q.v.).

form. **pallida** P. Junge ex Lüdi in Hegi, *l.c.*, 1751.

A form with flowers a very pale yellow, reported from banks of the Trave in N. Germany.

var. **praticola** (Domin) Lüdi in Hegi, *l.c.*, 1752. *P. officinalis* var. *praticola* Domin in Beih. Bot. Centralb. xxvi, 270 (1910), and in Act. Bot. Bohem., x, 175 (1931); *P. praticola* Fritsch, Exkursionsfl., Ed. 3, 393 (1922).

A plant smaller in all its parts than the type; scape less than 10 cm.; leaf only 4–7 cm., blade gradually narrowed into a very short broad-winged petiole. Found in Bohemia, on very old black meadows in the valley of the Middle Elbe. In a letter received in 1929 from Dr. Handel-Mazzetti, who had seen material, the opinion is expressed that the plant is not entitled to specific rank and in any case there is an earlier homonym.

var. **purpurascens** Diard ex Harrison, *l.c.*, 53, 61, 62, 75, 76.

Recorded from Corbridge in Durham by Harrison, who concludes from experimental evidence that the colour is not due to hybrid influence but to a mutation in nature involving flavine and anthocyanin pigments.

var. **tomentosa** Harrison, *l.c.*, 54.

This is a form with the leaves hoary-tomentose beneath. It is closely allied to *P. veris* subsp. *Columnae* (Ten.) Lüdi. Harrison was unable to find any tangible points to differentiate it from authentic *Columnae*, when he grew the two plants in his garden, but refrained from concluding they were identical. The variety is found dominant on coast sandhills in S.E. Durham.

form. **uniflora** (Hennings) Lüdi in Hegi, *l.c.*, 1751. *P. officinalis* f. *uniflora* Hennings in Schrift. Naturw. Ver. Schlesw. Holst., iv, 89 (1881); Pax, *l.c.*, 58. *P. officinalis* var. *uniflora* Goupil in Ann. Soc. Linn. Paris, iii, 252 (1825). *P. officinalis* var. *monantha* Schur, Enum. Pl. Transsylv., 553 (1866) ?

In this form the scape carries only one flower. It is recorded from France, Germany and possibly from Rumania.

P. veris subsp. **canescens** (Opiz) Hayek ex Lüdi in Hegi, Ill. Fl. Mittel-Eur., v, 1752 (1927); W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 42 (1928), and in Journ. Roy. Hort. Soc., liv, 21 (1929); Harrison in Trans. North. Nat. Union, i, 49, 74 (1931). *P. officinalis* var. *canescens* Opiz in Oekon. Techn. Fl. Böhm., ii, 2, 204 (1838); Beck, Fl. Niederösterreich, 915 (1893); Pax in Engl. Pflanzenr. Primulaceae, 58 (1905); Domin in Beih. Bot. Centralb., xxvi, 271 (1910); Journ. Roy. Hort. Soc., xxxix, 223 (1913); Hayek in Prod. Fl. Pen. Bal., ii, 24 (1928). *P. veris* var. *inflata* Reichb. Fl. Germ. Exc., 401 (1830). *P. inflata* Duby in DC. Prodr., viii, 36 (1844); Kerner in Österr. Bot. Zeitschr., xxv, 16 (1875). *P. veris* subsp. *inflata* var. *canescens* Domin in Act. Bot. Bohem., x, 176 (1931). *P. pannonica* Kerner, Schedae ad Fl. Aust. Hung., iv, 46 (1886). *P. officinalis* Fuss, Fl. Transsylv., 535 (1866)—*pro parte*; Schur, Enum. Pl. Transsylv., 553 (1866)—*pro parte*; Simonkai, Enum. Fl. Transsylv., 459 (1886); Willkomm et Lange, Prodr. Fl. Hisp., iii, 638 (1870). *P. veris* Bubani, Fl. Pyren., i, 222 (1897). *P. macrocalyx* Schur, Enum. Pl. Transsylv., 554 (1866). *P. officinalis* var. *inflata* Pax in Engl. Bot. Jahrb., x, 182 (1889). *P.*

officinalis var. *pannonica* Widmer, Europ. Art. Prim., 129 (1891).
P. suaveolens var. *montana* Rouy ex Lüdi l.c.

For separation from the normal plant see p. 439.

MINOR VARIATIONS IN SUBSP. *CANESCENS*.

form. **calvescens** (Pax) Lüdi in Hegi, l.c. *P. officinalis* var. *canescens* f. *calvescens* Pax, l.c., 59; Domin in Beih. Bot. Centralb., xxvi, 271 (1910). *P. officinalis* var. *canescens* f. *cetia* Beck, l.c. *P. veris* subsp. *inflata* var. *canescens* f. *viridis* (Opiz) Domin in Act. Bot. Bohem., x, 176 (1931).

A form with leaves glabrescent and greenish below, recorded from Austria, Hungary, Bohemia, and Silesia. Domin (l.c., 271) considers it a transition form to *P. veris* itself. Later (l.c., 176) he equates it with a variety of Opiz.

form. **cinerascens** Pax, l.c. Domin, l.c., 176.

Pax states that this form has the leaves grey-tomentose below and records it from Austria, Hungary, and Germany across to France and Spain. It is not referred to by Lüdi. Possibly not separable from subsp. *canescens*.

form. **composita** (Beck) Lüdi, l.c. *P. officinalis* var. *canescens* f. *composita* Beck, l.c.; Pax, l.c.

What Lüdi calls a monstrosity, with two superposed umbels, the upper one few-flowered. Has occurred in Lower Austria and no doubt elsewhere.

form. **hardeggensis** (Beck) Lüdi, l.c.; Beck, l.c.; Pax, l.c.; Domin, l.c.

A form with leaves densely white-tomentose below, found at Hardegg in Lower Austria and also in Bohemia. Both Domin and Lüdi consider it approaches subsp. *Columnae*.

form. **pseudo-columnae** Domin pro var. subspeciei **inflatae** in Act. Bot. Bohem., x, 176 (1931). *P. officinalis* var. *Columnae* Domin in Beih. Bot. Centralb., xxvi, 272 (1910), nec *P. Columnae* Tenore.

A Bohemian plant called by Domin a singular form of *inflata*, nearest to *canescens* but in its leaf shape and tomentum also like *Columnae*.

form. **subintegra** Domin, l.c., 271.

A Bohemian form with stiff almost entire leaves, thickly grey-tomentose below.

P. veris subsp. **Columnae** (Ten.) Lüdi in Hegi, *Illust. Fl. Mittel-Eur.*, v, 1752 (1927); W. W. Sm. & Forrest in *Notes Roy. Bot. Gard. Edin.*, xvi, 42 (1928), and in *Journ. Roy. Hort. Soc.*, liv, 21 (1929); Harrison in *Trans. North. Nat. Union*, i, 49, 54, 65, 74, 76 (1931); Domin in *Act. Bot. Bohem.*, x, 177 (1931). *P. Columnae* Ten. *Fl. Napol. Prodr.*, xxiv (1811), and *Fl. Nap., Atlas*, i, 54, t. 13 (1811-15); Kerner in *Österr. Bot. Zeitschr.*, xxv, 14 (1875); Beck in *Ann. Hof-mus. Wien*, ii, 144 (1887); *Journ. Roy. Hort. Soc.*, vii, 269, 278, 291 (1889); Pospichal, *Fl. Österr. Küstenland*, ii, 457 (1899); Halácsy, *Consp. Fl. Graec.*, iii, 6 (1904); *Journ. Roy. Hort. Soc.*, xxxix, 168, 171 (1913); Farrer, *Engl. Rock Gard.*, ii, 120, 163 (1928); Javorka and Csapody, *Ic. Fl. Hungar.*, 390 (1932); *Quart. Bull. Alp. Gard. Soc.*, iii, 108 (1935); *ibid.*, iv, 87 (1936); *ibid.*, viii, 108 (1940); Seligman, *ibid.*, ix, 192, with fig. (1941). *P. officinalis* var. *Columnae* (Ten.) Pax in *Engl. Bot. Jahrb.*, x, 182 (1889), and in *Engl. Pflanzenr. Primulaceae*, 59 (1905); Domin in *Beih. Bot. Centralb.*, xxvi, 272 (1910). *P. officinalis* subsp. *Columnae* (Ten.) Widmer, *Europ. Art. Prim.*, 130 (1891). *P. elatior* var. *Columnae* (Ten.) Reichb. *Fl. Germ. Excurs.*, 402 (1830). *P. suaveolens* Bertol. in Desvaux, *Journ. de Bot.*, 76 (1813); Lehmann, *Monogr. Primul.*, 25, t. 1 (1817) Reichb. *Icon. Fl. Germ.*, xvii, 35, t. 50, fig. 1 (1855); Koch, *Synops. Fl. Germ.*, Ed. 2, 693 (1846); Willkomm et Lange, *Prodr. Fl. Hisp.*, ii, 638 (1870); Boiss. *Fl. Orient.*, iv, 25 (1879); Simonkai, *Enum. Fl. Transsylv.*, 459 (1886); Caruel in *Parlatore, Fl. Ital.*, viii, 616 (1889). *P. veris* var. *suaveolens* (Bertol.) Reichb. *Fl. Germ. Exc.*, 401 (1830). *P. officinalis* var. *suaveolens* (Bertol.) Gren. et Godr. *Fl. France*, ii, 448 (1850); Velenovsky, *Fl. Bulgar.*, 477 (1891). *P. pyrenaica* Miègeville in *Bull. Soc. Bot. France*, x, 28 (1863). *P. Tommasinii* var. *Columnae* Caruel in *Parlatore, Fl. Ital.*, viii, 619 (1889). *P. cordifolia* Schur in sched. *P. discolor* Schur in sched.

For separation from the normal plant see p. 439.

MINOR VARIATIONS OF SUBSP. COLUMNAE.

form. **subvirescens** (Domin) Lüdi in Hegi, *l.c.* *P. officinalis* var. *Columnae* f. *subvirescens* Domin in *Beih. Bot. Centralb.*, xxvi, 272 (1910).

A form with more glabrous leaves, known from Czechoslovakia, Jugoslavia, Montenegro.

var. *valesiaca* Lüdi in Hegi, *l.c.*

Plants smaller; leaves short-stalked; under-surface greenish, with prominent nerves and less pronounced tomentum; hairs $\frac{1}{2}$ mm. long, numerous, stiff, glandular, $\pm$ as in *P. veris* itself; calyx 15 mm., wide at apex. Found near Martigny, Valais, Switzerland, on dry bushy slopes or dry meadows.

P. veris subsp. ***macrocalyx*** (Bunge) Lüdi in Hegi, *Illust. Fl. Mittel.-Eur.*, v, 1753 (1927); W. W. Sm. and Forrest in *Notes Roy. Bot. Gard. Edin.*, xvi, 42 (1928), and in *Journ. Roy. Hort. Soc.*, liv, 21 (1929); Harrison in *Trans. North. Nat. Union*, i, 49, 65, 74, 75 (1931). *P. macrocalyx* Bunge, *Fl. Altaica*, i, 209 (1829); Ruprecht in *Bull. Acad. St. Pétersbourg*, vi, 225 (1863); Boiss., *Fl. Orient.*, iv, 25 (1879); Kerner, *Schedae ad Fl. Austro-Hung.*, iv, 48 (1886); *Journ. Roy. Hort. Soc.*, xxxix, 168, 171 (1913); Grossheim, *Fl. Kavkaza*, iii, 205 (1932). *P. officinalis* var. *macrocalyx* (Bunge) C. Koch in *Linnaea*, xvii, 307 (1843); B. Beyer in *Abh. Bot. Ver. Brandenb.*, xxx, 322 (1888); Pax in *Engl. Bot. Jahrb.*, x, 182 (1889); Korshinsky in *Mém. Acad. St. Pétersbourg*, 8, ser. vii, 253 (1898); Kusnetzow, *Fl. Cauc. Crit.*, iv, 81 (1901); Pax in *Engl. Pflanzenr. Primulaceae*, 58 (1905); Turkevicz, *Fl. Ross. Asiat.*, 15 (1923); Busch in *Fl. Sib. et Orient. Extr.*, iv, Cem. 65, 23, figs. pp. 24, 26 (1926). *P. veris* Marsch.Bieb., *Fl. Taur. Cauc.*, i, 137 (1808). ? *P. inflata* Lehm. *Monogr. Primul.*, 26, t. 11 (1817); Duby in *DC. Prodr.*, viii, 36 (1844)—*pro parte*. *P. veris* subsp. *inflata* var. *macrocalyx* Domin in *Act. Bot. Bohem.*, x, 175 (1931). *P. officinalis* var. *inflata* Ledeb., *Fl. Ross.*, iii, 8 (1847-49); Regel in *Acta Hort. Petrop.*, iii, 132 (1874). *P. uralensis* Fischer ex Reichb. *Iconogr. Bot.*, vii, 18, t. 638 (1829). *P. officinalis* var. *infundibulum* C. Koch in *Linnaea*, xxiii, 617 (1850). *P. foliis rugosis* Gmelin, *Fl. Sibir.*, iv, 85, No. 32 (1769).

Note.—If Lehmann's description and figure of *P. inflata* could be clearly interpreted, it is possible that *P. macrocalyx* would become a synonym of Lehmann's Hungarian plant. From his description it would appear that Lehmann was not satisfied with the quality of his specimens, while the figure is far from convincing in the foliage, calyx, and corolla. Duby (*l.c.*) seems to be undecided; Pax (*l.c.*) enters a mark of interrogation; in recent years only Domin (*l.c.*) restores *inflata* as a subspecies and subjects both *macrocalyx* and *canescens* to it as vars.

For separation from the typical plant see p. 440.

MINOR VARIATIONS OF SUBSP. MACROCALYX.

form. **alpina** (O. Kuntze) Pax, *l.c.* *P. officinalis* var. *macrocalyx* f. *alpina* O. Kuntze in Acta Hort. Petrop., x, 210 (1887).

A dwarf form from the Caucasus with 2-5 subsessile flowers to the umbel.

form. **colchica** (Albow) Pax, *l.c.* *P. suaveolens* var. *colchica* Albow, Prodr. Fl. Colch., 167 (1895). *P. suaveolens* Radde, Grundzüge, 260, 357 (1899).

Like f. *virescens* this has an almost similar distribution to the subspecies and differs in the grey-tomentose under-surface of the leaves.

var. **montana** (Domin) Lüdi in Hegi, *l.c.* *P. officinalis* var. *montana* Domin in Beih. Bot. Centralb., xxvi, 270 (1910). *P. veris* subsp. *inflata* var. *montana* Domin in Act. Bot. Bohem., x, 176 (1931).

A very vigorous variety with the leaves including petiole up to 25 cm. and glabrous; the scape almost 40 cm.; calyx 16-20 mm., broadly and openly obconic; corolla-limb flat and pale yellow, 17-20 mm. across. Found in Bohemia.

form. **virescens** (Pax) Lüdi, *l.c.*; Pax, *l.c.*

This form appears to have nearly the same distribution as the subspecies and differs only in the leaves becoming green below.

P. veris subsp. **Velenovskyi** (Domin) Lüdi in Hegi, *Illust. Fl. Mittel-Eur.*, v, 1753 (1927); W. W. Sm. and Forrest in *Notes Roy. Bot. Gard. Edin.*, xvi, 42 (1928), and in *Journ. Roy. Hort. Soc.*, liv, 21 (1929); Harrison in *Trans. North. Nat. Union*, i, 49 (1931); *P. officinalis* var. *Velenovskyi* Domin in *Beih. Bot. Centralb.*, xxvi, 268, fig. 4b (1910), and sub *P. veri* in *Act. Bot. Bohem.*, x, 175 (1931). *P. Velenovskyi* Fritsch, *Exkursionsfl.*, Ed. 3, 393 (1922).

As no material of this plant is at present available, a short description taken from Domin (*l.c.*) is here given.

In height up to 30 cm. Leaves broadly ovate with a few narrower and oblong-ovate; blade 6-8 cm. long, 3-5 cm. broad, abruptly contracted (but not cordate) into a scarcely-winged petiole as long or longer, below greenish and almost completely glabrous, minutely

downy on the nerves. Scape slender, subglabrous, many-flowered with long pedicels. Calyx only 8–12 mm. long, broadly campanulate and open at apex; lobes broadly triangular, patent. Corolla small, deep golden-yellow; tube exceeds calyx. The plant is found in Bohemia in the valley of the Middle Elbe. To distinguish it from typical *P. veris*, Domin cites the leaf-form, the glabrousness and the short broadly campanulate calyx.

ADDENDUM.

At this point must be inserted a note to *P. legionensis* referred to on p. 439 as a possible subspecies. The type material in the herbarium of the British Museum is certainly meagre, but presents a facies alien to typical *P. veris*. In the circumstances it seems best to quote the original diagnosis of Wilmott.

P. legionensis, Wilmott in Journ. Bot., lxxvii, No. 797, 150 (1929).

P. veri affinis cum qua indumento et calycibus fructiferis plus minus congruit, sed ab ea foliorum laminis cordato-oblongis (circiter 7 cm. longis et 5 cm. latis), petiolis (c. 7 cm. longis) angustissime alatis solum 1.5–2 mm. latis.

Habitat in Prov. Legione, prope Riaño, 7 Jul. 1927; holotypus in Herb. Mus. Brit.

“A single specimen collected in fruit near Riaño has peculiar leaves with cordate-ovate laminae about as long as the narrow almost unwinged petiole. They are quite unlike those of any specimen of *Primula veris* or *P. elatior* I have ever seen, and resembling in a general way the summer leaves of an acaulescent *Viola*. Except at the apex they are only very slightly tomentose below, so it cannot be identified with *P. suaveolens*. The capsule is included in the inflated calyx, so it is either an aberrant form of *P. veris* or a new species.”

HYBRIDS OF *P. VERIS* L.

***P. veris* L. × *P. vulgaris* Huds.** Lüdi in Hegi, Ill. Fl. Mittel-Eur., v, 1786 (1927); Harrison in Trans. North. Nat. Union, i, 56 (1931).
P. acaulis × *P. officinalis* Ljungström in Bot. Centralb., xxxv, 182 (1888); Beyer in Abh. Bot. Ver. Brandenburg, xxix, 26 (1888); Pax in Engl. Bot. Jahrb., x, 184 (1889); Widmer, Eur. Art. Prim., 133 (1891). *P. officinalis* × *P. vulgaris* Grenier, Fl. Chaîne Jurass., 499 (1865–75). *P. officinalis* var. *genuina* ×

P. acaulis var. *genuina* Pax in Engl. Pflanzenr. Primulaceae, 63 (1905). *P. pseudoacaulis* Caruel in Parlatore Fl. Ital., viii, 610 (1889). *P. officinalis* var. *subacaulis* Döhl. Fl. Baden, 636 (1857) ?

= × **P. variabilis** Goupil in Ann. Soc. Linnéenne Paris, iii, 294, t. 4 (1825); Bailey in Journ. Bot., xli, 145 (1903); Lüdi in Hegi, l.c., 1786, fig. 2787 (1927). *P. brevistyla* DC. Fl. Franç., v, 383 (1815); Reichb. Ic. Pl. Germ., xvii, 35, t. 62 (1855); Kerner in Österr. Bot. Zeitschr., xxv, 77 (1875); Pax in Engl. Pflanzenr. Primulaceae, 63 (1905). *P. variabilis* var. *crenulata* et var. *expallens* Lange in Bot. Tidsskr., xiv, 157, 158 (1884-85). *P. intermedia* Facchini, Fl. Südtirol. in Zeitschr. Ferdinandeum 3, Folge v, 19 (1856) ? *P. Legueana* Camus in Bull. Soc. Bot. Fr., xxxvii, 174 (1890); Beck in Fl. Niederösterr., 916 (1893); Pax, l.c., 63 (1905).

This form of the cross approaches most closely to *P. veris*. There is a well-developed scape and the pedicels may be shorter, equal to or longer than the scape. It is recorded from England, Sweden, Schleswig-Holstein, France, Austria, etc.

There are other forms of this cross :

× **P. FLAGELLICAULIS** Kerner in Österr. Bot. Zeitschr., xxv, 79 (1875); Beck, l.c., 915; Pax, l.c., 63.

This form from Bornholm is more or less intermediate between the two parents. It has the scape about equal to the leaves and pedicels equalling or longer than the scape.

× **P. RADICIFLORA** Lange et Mortensen in Bot. Tidsskr., iii, Reihe 2, 237 (1877-79); Pax, l.c., 63. *P. variiflora* Beck, l.c., 914. From Sweden, Germany, France, and Austro-Hungary.

× **P. SANCTAE CORONAE** Beck, l.c., 914; Pax, l.c., 63. Recorded from Austria.

Both these forms clearly have most in common with *P. vulgaris*. They differ from each other chiefly in the degree of toothing of the calyx.

P. veris subsp. *canescens* (Opiz) Hayek × **P. vulgaris** Huds. Lüdi in Hegi, Ill. Fl. Mittel-Eur., v, 1787 (1927). *P. officinalis* var. *canescens* (Opiz) Beck × *P. acaulis* var. *genuina* Pax in Engl. Pflanzenr. Primulaceae, 63 (1905).

= × ***P. austriaca*** Wettstein in Kerner, Schedae ad Fl. Austr. Hung., iv, 49 (1886); Bailey in Journ. Bot., xli, 146 (1903); Pax, *l.c.*; Lüdi in Hegi, *l.c.*

This form of the cross from France and Austria is more or less intermediate between the two parents. The scape is longer than the leaves, there are no basal solitary flowers and the pedicels are elongate. The leaves are greyish-purple below.

Other forms of this cross are:

× ***P. GAISBERGENSIS*** Pax, *l.c.*, 64. This Austrian plant is nearer to *P. veris* subsp. *canescens*. There are no basal flowers. All are borne on a scape longer than the leaves and are small and semi-nodding. The pedicels are much shorter than the scape.

× ***P. RICHTERI*** Pax, *l.c.*, 63—with the same pubescence as the following but with the flowers always carried on a scape.

× ***P. WIESBAURII*** Pax, *l.c.*, 63—with the leaves having an ashy-coloured pubescence below and the flowers either on a short scape or arising solitary at the base.

These two Austrian forms approach most closely to *P. vulgaris*.

P. veris* subsp. *Columnae (Ten.) Lüdi × ***P. vulgaris*** Huds. Lüdi in Hegi, Ill. Fl. Mittel-Eur., v, 1787 (1927). *P. officinalis* var. *Columnae* (Ten.) Pax × *P. acaulis* var. *genuina* Pax in Engl. Pflanzenr. Primulaceae, 64 (1905).

= × ***P. ternoviana*** Kern. in Österr. Bot. Zeitschr., xxv, 77 (1875); Bailey in Journ. Bot., xli, 146 (1903); Pax, *l.c.*, Lüdi in Hegi, *l.c.* *P. travnicensis* Wiesbaur in Österr. Bot. Zeitschr., xxxii, 282 (1882); Beck in Ann. Hofmus. Wien, xiii, 5 (1898). *P. bosnaica* Beck in *ibid.*, ii, 126 (1887); *ibid.*, xiii, 4, 5 (1898); Fiala in Glasn. Zemaljsk. Muz., iii, 30 (1891). *P. variabilis* Caruel in Parlatore, Fl. Ital., viii, 611 (1889).

P. ternoviana is that form of the hybrid more or less intermediate between the two parents. All the flowers are produced on a well-developed scape as long as or even longer than the leaves, which are quite thickly greyish-tomentose on the lower side. A native of Switzerland, France, Italy, and Bosnia.

The form of the hybrid most nearly approaching *P. veris* subsp. *Columnae* is known as

× ***P. TOMMASINII*** Godr. et Grenier, Fl. France, ii, 449 (1852); Reichb. Icon. Fl. Germ., xvii, 41, t. 61 (1855); Willkomm et

Lange, Prodr. Fl. Hisp., ii, 639 (1870); Caruel, *l.c.*, 618, excl. var. β ; Beck, *l.c.*, xiii, 4, 6 (1898); Pax, *l.c.*; Lüdi, *l.c.* *P. officinalis* subsp. *Columnae* var. *Tommasinii* Widmer Eur. Art. Prim., 130 (1891). *P. macedonica* Adamovic in Kneucker, Allg. Bot. Zeitschr., xi, 3 (1905).

Native of the Pyrenees, Italy, Bulgaria, Armenia, this form has citron-yellow flowers, with five orange-coloured spots around the throat.

Several forms of the hybrid are obviously nearer to *P. vulgaris* than the other parent:—

× *P. AMBIGUA* Beck, *l.c.*, xiii, 4, 5; Pax, *l.c.*

From Bosnia, as well as from Switzerland, this plant is much like the following but has additional basal flowers.

× *P. BRANDISII* Wiesbaur, *l.c.*; Beck, *l.c.*, 35; Pax, *l.c.*

Also native of Bosnia, this plant possesses a very short scape with flowers smaller than those of *P. vulgaris*. There are no basal flowers and the leaves are ashy-tomentose beneath.

× *P. TOMENTOSA* (Beck) Pax, *l.c.* *P. acaulis* var. *tomentosa* Beck, *l.c.*, ii, 144 (1887); *ibid.*, viii, 5 (1898).

Another Bosnian plant, this time a secondary hybrid, scapeless, and with leaves white-tomentose below and on short contracted petioles.

P. veris L. × **P. vulgaris** subsp. **Sibthorpii** (Hoffmannsegg) W. W. Sm. et Forrest. *P. veris* subsp. *genuina* × *P. vulgaris* var. *rubra* Lüdi in Hegi, Ill. Fl. Mittel-Eur., v, 1787 (1927). *P. acaulis* var. *rubra* × *P. officinalis* var. *genuina* Pax in Engl. Pflanzenr. Primulaceae, 65 (1905).

= × **P. anglica** Pax, *l.c.*; Lüdi in Hegi, *l.c.*

This well known cultural form of the hybrid is more or less intermediate between the two parents. It has red or purple flowers with long pedicels, carried on a scape at least as long as the leaves.

Much nearer *P. veris* is

× *P. TRISTIS* Pax, *l.c.*; Lüdi in Hegi, *l.c.*

Another familiar garden form with dull purple flowers smaller than those of *P. veris* and with much shorter pedicels than those of *P. anglica*.

P. veris subsp. **macrocalyx** (Bunge) Lüdi $\times$ **P. vulgaris** Huds. Lüdi in Hegi, Ill. Fl. Mittel-Eur., v, 1787 (1927). *P. officinalis* var. *macrocalyx* (Bunge) C. Koch $\times$ *P. acaulis* var. *genuina* Pax in Engl. Pflanzenr. Primulaceae, 63 (1905). *P. acaulis* $\times$ *macrocalyx* Pax in Engl. Bot. Jahrb., x, 185 (1889).

= $\times$ **P. cupularis** Pax, *l.c.*; Lüdi in Hegi, *l.c.*

A Silesian plant, one time cultivated in the Breslau Botanic Garden, having an inflated funnel-shaped calyx.

P. vulgaris Hudson, Fl. Angl., Ed. 1, 70 (1762); Walcott, Fl. Brit. Indig., t. 16 (1778); Sowerby & Sm., Eng. Bot., i, t. 4 (1790); Jackson, Pict. Fl., fig. 305 (1840); Deakin, Florigr. Brit., i, fig. 322 (1841); Loudon, Ladies' Fl.-Gard. Ornam. Perenn., ii, t. 94 (1844)—*P. acaulis* in textu, p. 159; Loudon, Brit. Wild Fl., Ed. 2, t. 46 (1846); T. Moore, Field Bot. Comp., t. 4 (1862); Hogg & Johnson, Wild Fl. Gt. Brit., ii, t. 101 (1864); Bentham, Handb. Brit. Fl., fig. 642 (1865); Syme, Engl. Bot., vii, t. 1129 (1867); Hulme, Plant Form, t. 87 (1868); Willkomm et Lange, Prodr. Fl. Hisp., ii, 637 (1870); Pratt, Fl. Pl. Grasses, Sedges and Ferns of Great Brit., Ed. 3, iv, t. 168 (1873); Hulme & Hibberd, Familiar Gard. Fl., iv, t. 93 (1879–87); Favart, Flowers and Pl., t. 6 (1860); M'Alpine, Bot. Atlas, i, t. 22 (1883); Nicholson, Illust. Dict. Gard., iii, 223 (1884–88); Caruel in Parlatores, Fl. Ital., viii, 607 (1889); Journ. Roy. Hort. Soc., vii, 234, 269, 275–277, 282, 287, 289, 291, 292, fig. 23 (1889); Step, Fav. Fl. Gard. and Greenh., iii, t. 171 (1892); Gard. Chron., xvii, 593 (1895); The Garden, liv, 142 (1898); C. T. Green, Fl. Liverpool Distr., fig. 403 (1902); T. G. Hill in Ann. of Bot., xvi, 319 (1902); Coste, Fl. France, ii, 522 (1903); Step, Wayside and Woodland Bloss., ii, t. 30 (1905); Merino, Fl. Galicia, ii, 26 (1906); Lazaro, Comp. Fl. Españ., ii, 597 (1907); Hulme, Familiar Swiss Fl., t. 61 (1908); Journ. Roy. Hort. Soc., xxxviii, proc. p. ccxxxvi (1912); *ibid.*, xxxix, 100, 101, 227 (1913); Perrin and Boulger, Brit. Flower Pl., iii, t. 208, 214, figs. 1–10 (1914); Horwood, Brit. Wild Fl., i, 147; iii, t. 21 (1919); Fitch and Smith, Ill. Brit. Fl., Ed. Rev. 4, Iss. 2, fig. 650 (1919); Dallman in Journ. Bot., 316 (1921); Lindman, Bild. Nord. Fl., Ed. 2–3, Suppl., t. 582 (1926); Hegi, Ill. Fl. Mittel-Eur., v, 1743, figs. 2740–2742 (1927); W. W. Sm.

and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 42 (1928), and in Journ. Roy. Hort. Soc., liv, 21 (1929); Harrison, Trans. North. Nat. Union, i, 48-76 (1931); Javorka and Csapody. Iconogr. Fl. Hungar., 390 (1932); Gard. Chron., cii, fig. p. 91 (1937); Valentine in New Phyt., 46, 229 (1947). *P. acaulis* (L.) Hill. Veg. Syst. viii, 25 (1765); Oeder, Fl. Dan., 194 (1767); Jacq. Misc. Austr., i, 158 (1778); Schmidt, Fl. Boem., ii, 43, t. 167 (1793); Bot. Mag., t. 229 (1793); Curtis, Fl. Londin., ii, fasc. vi, t. 16 (1798); *ibid.*, Ed. 2, iii, fasc. vi, t. 16 (1826); Boissier, Fl. Eur., i, t. 121 (1805); Lehmann, Monogr. Primul., 30 (1817); Koch, Synops. Fl. Germ., Ed. 1, 587 (1837); Maund, Bot. Gard., i, t. 15 (1825-26); *ibid.*, xiii, t. 299 (1839-51); Ledeb. Fl. Ross., iii, 10 (1847-49); Cassone. Fl. Med.-Farm., v, t. 444 (1850); Regel in Acta Hort. Petrop., iii, 133 (1874); The Garden, ix, 396 (1876); *ibid.*, xiii, 455 (1878); *ibid.*, xv, 406 (1879); *ibid.*, xxviii, 538 (1885); *ibid.*, liii, 309 (1898); Gartenfl., xxvii, 24 (1878); Boiss. Fl. Orient., iv, 24 (1879); Schlechtendal, Lang. & Schenk, Fl. Deutschl., Ed. 5, xix, t. 1966 (1884); Pax in Engl. Bot. Jahrb., x, 180 (1889); Journ. Roy. Hort. Soc., vii, 169-173, 205-206, 269, 275, 277, 279-281, 288, 291-293 (1889); Widmer, Eur. Art. Prim., 126 (1891); Bot. Centralbl., xiv, lv, 226 (1893); Miller Christy in Journ. Linn. Soc., xxxiii, 172 (1897); Sturm, Fl. Deutschl., Ed. 2, ix, t. 61 (1901); Fiori and Paol. Ic. Fl. Ital., 313 (1901); Kusnetzow, Fl. Cauc. Crit., iv, 76 (1901); Bailey, in Journ. Bot., xli, 145 (1903); Halácsy, Consp. Fl. Graecae, iii, 6 (1904); Pax in Engl. Pflanzenur. Primulaceae, 54 (1905); Rev. Hort., 144 (1907); Heukels, Fl. Nederl., iii, 38, 39 (1909); Correvoon, Fl. Champs et Bois., t. 1 (1911); Gartenwelt, xv, 270 (1911); Francé, Leben Pflanze., vi, 132 (1913); Journ. Roy. Hort. Soc., xxxix, 100, 167-169, 171-172, 219, 222, 224, 226-227, 812 (1913)); *ibid.*, xlv, proc. p. xlii (1919); *ibid.*, liv, 21, 42, 95 (1929); *ibid.*, lvi, proc. p. ix (1930); *ibid.*, lviii, 231 (1933); Gard. Chron., lxxi, 145 (1922); *ibid.*, lxxxiii, 352 (1928); Farrer, Engl. Rock Gard., ii, 106 (1919); Macwatt, Prim. of Europe, 27 (1923); Buxton in Journ. Genetics, xxv, 195-205, pl. vi (1932); Scott-Moncrieff, *ibid.*, 206-210 (1932); H. S. Losin-Losinskaja in Bull. Acad. Sc. U.S.S.R., Ser. vii, 293 (1933); Gard. Chron., cii, 215 (1938). *P. acaulis* var. *genuina* Pax in Engl. Bot. Jahrb. x, 180 (1889), and in Engl. Pflanzenur. Primulaceae, 54 (1905). *P. acaulis* var. *parviflora* et var. *grandiflora* C. Koch in Linnaea, xxiii, 618 (1850). *P.*

vulgaris subsp. *genuina* (Pax) Harrison in Trans. North. Nat. Union, i, 50 (1931). *P. vulgaris* var. *genuina* (Pax) Beauverd in Bull. Soc. Bot. Geneve, Ser. 2, ix, 371 (1917). *P. veris* var. *acaulis* L. Sp. Plant., Ed. 1, i, 143 (1753). *P. sylvestris* Scop. Fl. Carn., Ed. II, i, 132 (1772); Reichb. Iconogr., xvii, 41, t. 50, f. ii, iii (1855). *P. grandiflora* Lam. Fl. Franç., ii, 248 (1778); Duby in DC. Prodr., viii, 37 (1844); Godron et Grenier, Fl. France, ii, 447 (1852). *P. hybrida* Schrank, Bayr. Fl., 449 (1789). *P. vernalis* Salisb. Prodr. Stirp. Chapel Allerton, 117 (1796). *P. uniflora* Gmel. Fl. Badens., i, 442 (1805); Stokes, Bot. Mat. Med., i, 290 (1812). *P. bicolor* Rafinesque, Caratt. g. nouov. gen. 78 (1810).

The early history of *P. vulgaris* is interwoven with that of its allies *P. elatior* and *P. veris*. Up to the time of Linnaeus the three were recognised as varieties of one specific unit. To Linnaeus the plant was known as *P. veris* var. *acaulis*. But for at least two centuries earlier some degree of distinction was noted between the three. *P. vulgaris* was referred to by Bauhin (Phytopinax, 460 (1596) as *Verbasculum sylvarum majus singulari flore*. Clusius knew it as *P. veris pallido flore humilis* (Rar. Plant. Hist., iii, 302 (1601)). In literature the name *P. acaulis* has been used even more frequently than *P. vulgaris*. The word *acaulis* has been associated with it earlier than *vulgaris*, but the latter was the first to be used as the specific epithet and so has priority.

This species occupies almost as wide an area as either of its two allies. It is found in the west coastal parts of Mid-Norway, in Denmark, from Mecklenburg westwards in the maritime regions to Holland and Belgium, throughout the British Isles and in most of France, in N.W. Spain to the south of Portugal, in Corsica, in Italy and Sicily, in the south-west and south of Switzerland, throughout the Balkan peninsula including Greece and the islands, on the northern shores of Asia Minor to the Caucasus and the Crimea; also in Syria, Armenia, and in North Africa. It is absent or only sparingly found in Central Europe and in Russia, common in many areas south of the Danube, more sporadic to the north of it. A very good map of the distribution is given by Lüdi (*l.c.*, 1744). In the main the area is represented by the maritime regions of West Europe, by the countries to the north of the Mediterranean, and by the Caucasus with Asia Minor. It does not follow from this apparent addiction to maritime countries that the species is restricted to lowland situations. It may be frequent just above sea-level, but

it reaches 660 m. in the British Isles, 1000–1500 m. in Switzerland, 1100–1700 m. in Greece, while heights up to 2500 m. have been recorded from the Caucasus.

Although *P. vulgaris* inhabits an extensive territory, it does not show any very significant deviations from what may be termed the normal plant. Throughout practically the whole area the typical plant prevails, with occasional fluctuations in leaf-shape, in degree of pubescence, and in colour of flower. The under-surface of the leaves shows on the veins prominent hairs, which also beset the angles of the calyx. The dominant colour of the flower is yellow, with the sporadic occurrence of white or purple. Of the subspecies the most distinct appears to be subsp. *Sibthorpii*, native to the eastern Mediterranean region, including the Caucasus and North Persia. In it the dominant colour is purple or rose. Near it geographically is the Caspian Primula, subsp. *heterochroma*, where the corolla has a wide range of tints but with no colour dominant. In certain isolated cases the evidence favours the view that a white colour may be dominant as in subsp. *balearica* and subsp. *Ingwerseniana*, as also in var. *atlantica* and var. *pulchella*. Colour distinctions are not always satisfactory criteria, but there is no doubt that over wide areas certain definite colours in Primula are exclusively dominant and constant or almost so.

Stapf in Bot. Mag., t. 9166, has a pertinent note—too long to quote here—showing how *P. vulgaris* may have developed from tertiary times, with slight morphological modifications going hand in hand with the fixing of the colours, accentuating the differentiation of this primrose into its present-day components. Germane to the same problem are the experiments and observations on *P. vulgaris* and its allies by Harrison in Trans. North. Nat. Union, i, 58–63 (1931). In the same publication will be found the results of Harrison's work on the pollination of the British species. The same subject is dealt with by Miller Christy in Journ. Linn. Soc., xlv, 105 (1922), and also by Dallman in Journ. Bot. lix, 316, 337 (1921). *P. vulgaris* as a rule has no scape, and the flowers arise singly on long pedicels from the base of the plant. This character separates it readily from all the other members of the section except *P. Juliae*, which, however, can be recognised at once by the small orbicular leaves. *P. vulgaris* may sometimes develop a scape; see under var. *caulescens*.

A hairy perennial with a short stout rhizome, surrounded at the apex with a few basal remains of old leaves and furnished with numerous rather fleshy roots. Leaves arranged in a loose rosette,

including the petiole 5–25 cm. long, 2–6 cm. broad; lamina oblanceolate to obovate, rounded at the apex, gradually tapering at the base into the petiole, irregularly erose-denticulate to crenate at the margin, membranous in texture, glabrous above, more or less pilose on the veins below; veins impressed above, mid-rib and 8–10 pairs of lateral nerves prominent below; petiole usually short and hardly separable from lamina, occasionally almost subequal to it, always membranously winged and broad and sheathing at the base. Scape absent; bracts hidden among the bases of the leaves, 1–1.5 cm. long, linear to linear-lanceolate, attenuate at the apex; pedicels when fully developed 6–20 cm. long, covered with long soft septate hairs. Calyx 1–2 cm. long, tubular, prominently 5-angled and 5-nerved, strongly pilose along the angles, cut to a third or nearly to a half into lanceolate acuminate teeth. Corolla pale yellow with an orange spot at the base of each petal, annulate or exannulate, heteromorphic; tube as long as or a little longer than calyx, cylindrical, slightly ampliate above insertion of stamens; limb 2–4 cm. in diameter with patent overlapping emarginate lobes. Stamens, with anthers 2 mm. long, inserted at apex of corolla-tube, or nearly so, in thrum-eyed flowers, near the middle of tube in pin-eyed. Long style as long as corolla-tube or a little shorter; short style half the length of tube. Capsule ovate to ovate-ovoid, two-thirds the length of calyx, being brought to the surface of the ground at maturity by the bending of the pedicels. Seeds 2–2.5 mm. in diameter, globose or irregularly ovoid, brown, vesicular-surfaced.

MINOR VARIATIONS AND FORMS OF *P. VULGARIS*.

(These are of unequal status and some are trivial.)

var. **alba** Goup. in Mém. Soc. Linn. Paris, iii, 247 (1825); Harrison in Trans. North. Nat. Union, i, 51 (1931).

Instead of the usual pale yellow flowers with the orange spots at the base of the corolla-lobes, the flowers of this variety are whitish, still retaining the orange marking. The occurrence of white forms can be traced back as far as the time of Bauhin. There are also white horticultural forms common in cultivation.

form. **angustiloba** Ljungström in Botanisker Not., 1885, p. 123, fig. p. 128, et in Bot. Centralbl., xxxv, 181 (1888); Beauverd in Bull. Soc. Bot. Genève, Ser. 2, ix, 362, fig. p. 365 (1917). *P.*

vulgaris subsp. *angustiloba* Gerbault in Bull. Soc. Amis Sc. Nat. Rouen, 183-191 cum fig. (1918). *P. vulgaris* subsp. *stenopetala* Harrison in Trans. North. Nat. Union, i, 52 (1931), cum var. *pallidiflora* et var. *rubriflora*.

This form has the corolla-lobes neither overlapping nor touching but separate and quite narrow. Certain very minor fluctuations in the chief members of the Vernales have been noted for over a century until the present time in the shape of the leaf, the number of flowers, the length of the calyx, the breadth of the corolla-tube and of the lobes, the heteromorphy, etc. Many of these have been given definite names generally as varieties or forms. There are numerous examples in the work of Opiz in Fl. Böhmens, iii, 195-205 (1839). In some respects this analysis is carried further by Ljungström (*l.c.*, 123), who finds f. *latiloba* and f. *angustiloba* not only in *P. elatior*, *P. veris*, and in *P. vulgaris*, but also in *P. farinosa*, *P. scotica*, *P. stricta*, and *P. sibirica*. (To that list many additions could easily be made.) Beauverd (*l.c.*) refers to Ljungström's work, accepts his terms, and in describing a new variety *truncata* (q.v.) records that it too has a form *angustiloba* and a form *latiloba* as well as f. *brevicalyx* and f. *longicalyx*. Gerbault (*l.c.*) cites no other author, uses the same term *angustiloba*, and calls this plant a subspecies in one part of the text and later an elementary species, as is also *P. vulgaris*.

Ljungström's publications deal in great part with his observations on the Danish island of Möen, and contain a list of his forms which it is expedient to deal with here. Some require no further comment.

f. *brevicalyx* Ljung.

f. *colorata* Ljung. With purple-violet corolla. Probably =f. *purpurea* Maulny. Pax (*l.c.*, 56) equates it with his *P. acaulis rubra* (geographically most unlikely).

f. *lactea* Ljung. Pax, *l.c.*, 55. Why not the same as var. *alba* Goup.?

f. *latiloba* Ljung. The fig. in Beauverd (*l.c.*) represents the familiar form.

f. *longicalyx* Ljung.

In no instance does it seem necessary to give any one of them a higher status than that of a form, and some do not merit even that.

var. **atlantica** Maire et Wilczek in Bull. Soc. Hist. Nat. Afrique du Nord, xxii, 55 (1931).

According to the original diagnosis this variety is distinguished from the typical *P. vulgaris* by the white flower with yellow throat and yellowish tube and by the 5-winged (not 5-ribbed) calyx. The authors point out that it approaches var. *balearica* in colour of flower but differs in the leaves glabrous above and long and diffusely villous on the nerves below; also in the shorter and more broadly winged petiole. It is found near springs in Cedar forests in the Algerian Atlas above the town of Blida at 1300–1450 m.

Where white-flowered plants occur sporadically in company with dominant *P. vulgaris* they are usually assessed as colour-forms. Where white-flowered plants are without admixture as in the Balearic Islands or in Andros and thus removed geographically, the tendency is to accord them a higher status. The line between subspecies and variety is often finely drawn. How far any of these white-flowered expressions of the aggregate *P. vulgaris* are equivalent *inter se* is a problem yet unsolved.

var. **calva** Beauverd in Bull. Soc. Bot. Genève, Ser. 2, ix, 370 (1917).

This form is quite glabrous except for a sparing puberulousness only to be seen under a lens. It is found in Turkey-in-Asia, usually in subalpine calcareous habitats at 1000–1400 m. In its glabrous character but not in its yellow flowers it invites comparison with var. *pulchella* (q.v.) from the island of Andros. Beauverd notes that *cette forme* occurs in company with *P. vulgaris* itself.

var. **caulescens** (Koch) Miller Christy in New Phyt., xxii, 233 (1923); Harrison in Trans. North. Nat. Union, i, 51 (1931). *P. acaulis* var. *caulescens* Koch, Synops. Fl. Germ., 585 (1837); Neilreich, Fl. Niederöster., 584 (1858); Pax in Engl. Bot. Jahrb., x, 180 (1889). *P. vulgaris* f. *caulescens* (Koch) Schinz et Thellung ex Lüdi in Hegi, Ill. Fl. Mittel-Eur., v, 1745 (1927). *P. pseudo-acaulis* Schur, Enum. Pl. Transsylv., 552 (1866). ? $\times$ *P. caulescens* (Koch) Pax in Engl. Pflanzenr. Primulaceae, 61 (1905)—*pro parte*. *P. acaulis* f. *umbellifera* Beck in Fl. Niederöster., 913 (1890); Pax, *l.c.* 55.

This variety has been found in Germany, Austria, Switzerland, France, and Great Britain. It has a well-developed scape with an umbel of flowers. But two very similar plants have been confused under the same name. One is a variety of *P. vulgaris* itself. The

other is a hybrid with *P. veris* as the other parent. A very complete exposition is given by Miller Christy (*l.c.*), who points out that the former has been known in Britain since 1792. The fortuitous development of the scape, in species normally acaulescent, occurs elsewhere in the genus.

var. **hypoleuca** Beauverd in Bull. Soc. Bot. Genève, Ser. 2, ix, 372 (1917). *P. acaulis* var. *hypoleuca* Halácsy, Conspec. Fl. Graecae, iii, 6 (1904); Pax in Engl. Pflanzenr. Primulaceae, 55 (1905), in nota.

Halácsy indicates that this Greek plant is a variety or form with the under-surface of the leaves finely hoary-tomentose. Beauverd's note contains merely a change in nomenclature.

var. **obscura** Harrison in Trans. North. Nat. Union, i, 51 (1931).

This variety is common near the coast in Northumberland and Durham, but also occurs elsewhere. The leaves are markedly of a darker grey-green in colour than in the type.

var. **pulchella** (Heldr.) nom. nov. *P. acaulis* var. *pulchella* Heldr. in Supplem. Secund. Conspec. Fl. Graec., 72 (1912).

Briefly described by Heldreich as a plant with smaller flowers, of a pale colour, elegantly ocellate at the throat with orange spots. It is recorded from the island of Andros in the Cyclades, growing in shady spots by thin trickles of water. A specimen in the Edinburgh Herbarium collected by P. Davis in April 1938 in Andros bears the statement: "Leaves glabrous. Corolla white with a large and distinct centre."

In its white flowers it invites comparison with subsp. *balearica* and subsp. *Ingwerseniana*, but the calyx is quite glabrous as are the leaves. This variety may well merit the same status as these two allies. Mr. Davis informs us that he collected on Andros a form of it with purple flowers and similarly glabrous.

var. **purpurea** Maulny, Plantes observées aux environs de la ville du Mans, 193 (1786); Harrison in Trans. North. Nat. Union, i, 51 (1931). var. *purpurascens* Goup. in Ann. Soc. Linn. Paris, iii, 247 (1825). ?*P. acaulis* f. *colorata* Ljungström in Bot. Centralbl., xxxv, 181 (1888).

This variety forms 60 per cent. of the *vulgaris* population in Pembrokeshire. It is also present as a casual and in more or less populous colonies in Northumberland and Durham. The flowers are purplish

to liver-coloured. This variety occasionally produces a well-developed scape, and such wild caulescent plants are recorded from Pembrokeshire.

var. **rubescens** Harrison in Trans. North Nat. Union, i, 51 (1931).

It is thus recorded: "Base of leaves, pedicels, and calyx strongly charged with one or more anthocyanin products. Locally from Gibside Woods and near Birtley; occasionally from the coast. The whole of the plants secured from Torquay belonged to this variety."

var. **sileniflora** Murr ex Lüdi in Hegi, Ill. Fl. Mittel-Eur., v, 1745 (1927).

Lüdi calls this an abnormality with the corolla divided to the base into free segments. Collected by Murr in 1901 in the neighbourhood of Doss Trento. (Not to be confused with $\times$ *P. sileniflora* H. Schmidt—a hybrid between *P. elatior* and *P. veris* with the corolla also divided to the base. See Pax in Engl. Pflanzenr. Primulaceae. 61 (1905).)

var. **truncata** Beauverd in Bull. Soc. Bot. Genève, Ser. 2, ix, 362, figs. p. 365 (1917)—cum formis *longicalyx*, *brevicalyx*, *latiloba*, *angustiloba*.

This variety differs from the type in having truncated petals. The names of the forms are those used by Ljungström. See under *f. angustiloba*, p. 456.

form. **viridiflora** Druce in Bot. Exchange Club Brit. Isles, 446 (1925).

A curious plant found in June 1924 at Inverary, Argyll. Druce gives this note: "The corolla is of a very pale green colour with a yellow throat. The corolla-lobe margins are slightly crenulate as noticed by the sender, the under side of the corolla is faintly rugose and clothed with slight arachnoid pubescence. It is evidently a foliaceous corolla, but with a texture on the upper side nearly glabrous and having the normal shape of a Primrose blossom."

var. **viridimaculata** Harrison in Trans. North. Nat. Union, i, 51 (1931).

A Northumberland and Durham variety, gathered by Harrison in Dipton Woods, Blackhall Rocks, Belsay, and other localities. Instead of the blotches at the base of the corolla-lobes being orange, they are bright green.

P. vulgaris subsp. **balearica** (Willkomm) W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 42 (1928), and in Journ. Roy. Hort. Soc., liv, 21 (1929); Harrison in Trans. North. Nat. Union, i, 48, 63, 66, 74-75 (1931); Cooke in Quart. Bull. Alp. Gard. Soc., ii, 309, with fig. (1934); *ibid.*, iii, 158 (1935). *P. vulgaris* var. *balearica* Willkomm in Linnaea, xl, 75 (1876), and in Illust. Fl. Hispan., i, 52, t. 35 (1881-85); Pax in Engl. Bot. Jahrb., x, 181 (1889); Widmer, Eur. Art. Prim., 127 (1891); Pax in Engl. Pflanzenr. Primulaceae, 55 (1905); MacWatt, Primulas of Europe, 12, 28 (1923); Farrer in Eng. Rock Gard., ii, 106 (1928).

According to Willkomm (*l.c.*, 52), this plant was first discovered by Barcelo in the island of Majorca growing at 1500 m. among rocks on the Puig de Torella. Willkomm visited the locality in 1873 and collected the plant in full flower in the first week of May. It grows at the bottom of small hollows which are filled with snow until April. He notes that this white Majorca Primula is the only member of the genus to be recorded from the Balearic Isles, and distinguishes it from *P. vulgaris* by the large snow-white corolla, by the narrowly winged petioles, by the leaves glabrescent below, and by the more pronounced scent. He suggests that it may yet be regarded as a distinct species. His second diagnosis is accompanied by a fine plate and supplies the following measurements: Leaves and petiole 10-16 cm.; blade alone 3-4 cm.; peduncles 9-12 cm.; corolla 3 cm. broad. Plants in culture show that these data must be interpreted widely, for the short leaf-blade may yet be longer than the well-winged petiole, somewhat hairy above and never quite glabrous below, and the peduncles often of very moderate length. The subspecies was here in gardens before the war and is reckoned hardy. At this date a few may have survived. It crosses readily with certain members of the section (Harrison, *l.c.*).

While white flowers may occur fortuitously in the realms of *P. vulgaris*, there is here a clear case of geographical isolation and the status of subspecies may be merited. The plant invites comparison with subsp. *Ingwerseniana*, with var. *pulchella*, and with var. *atlantica*, with none of which is it quite in agreement.

P. vulgaris subsp. **heterochroma** (Stapf) W. W. Sm. and Forrest in Notes Roy. Bot. Gard. Edin., xvi, 42 (1928), and in Journ. Roy. Hort. Soc., liv, 21 (1929); Harrison in Trans. North. Nat. Union, i, 62, 74, 75 (1931); Journ. Roy. Hort. Soc., lvi, 153 (1931). *P. vulgaris* var. *heterochroma* Stapf in Bot. Mag.,

t. 9166 (1929). *P. heterochroma* Stapf in Denkschr. Akad. Wiss. Wien, i, 70 (1885); Pax in Engl. Bot. Jahrb., x, 181 (1889), and in Engl. Pflanzenr. Primulaceae, 56 (1905); Journ. Roy. Hort. Soc., vii, 273 (1889); Balf. f., *ibid.*, xxxix, 167, 168, 171, 172 (1913); Grossheim, Veg. and Fl. Talysch-Geb. in Beih. Bot. Centralbl., xliii, 2, pp. 1, 7, 8, 19 (1927), et in Fl. Kavkaza, iii, 207 (1932) cum var. *flava* Grossh. et var. *violacea* Grossh. Farrer, Eng. Rock Gard., ii, 139 (1928). *P. acaulis* Hohenacker, Enum. Pl. Elisabethpol in Bull. Soc. Nat. Mosc., vi, 220 (1833); Buhse and Boiss. Aufzähl. Transkauk. and Pers. Pflanz., 144 (1860); Lomakin, Spec. Rast. Talysch in Trud. Tifles. Bot. Sad., i, 60 (1895), haud alior. *P. acaulis* var. *genuina* Chelkovnikoff, Excurs. Talyche in Monit. Jard. Bot. Tifles, Livr., 3, pp. 9, 14 (1906), haud alior. *P. acaulis* var. *rosea* Lom., *l.c.* (1895), haud Boiss. *P. acaulis* var. *Sibthorpii* Chelk., *l.c.* (1906), haud alior. *P. amoena* var. *acaulis* C. A. Meyer in Verzeichn. Pflanz. Caucas., 114 (1831); Hohenacker, Enum. Pl. Talysch, in Bull. Soc. Nat. Mosc., 317 (1838).

The material on which Stapf based his diagnosis of this plant was collected in flower in April 1882 by Pichler in N. Persia. There is evidence given by Stapf (Bot. Mag., *l.c.*) that it is the same as specimens obtained by Buhse in 1849, also in N. Persia, and attributed by Kusnetzow to *P. vulgaris*. The status of the plant, as the literature shows, has been variously assessed—as a species, a subspecies, or as a variety. Good examples of it were in culture in this country during 1928–32, and the opportunity was taken by Stapf (Bot. Mag.) to give a complete and most satisfactory analysis of it. He discriminates it from the other subspecies of *P. vulgaris* by the leaf-blades being softly cobwebby-tomentose below and generally shortly and abruptly contracted into a narrowly winged petiole which ultimately considerably lengthens, as well as by the colour of the flower which may be white, rose, purple, violet or citron-yellow. Stapf points out that these colours, except yellow, may all occur sporadically in the domain of *P. vulgaris* but are not dominant, whereas in subsp. *heterochroma* no one colour, not even yellow, has gained the mastery. For his pertinent notes thereon, reference must be made to his paper.

The subspecies is apparently confined to N. Persia, to two provinces bordering the south shores of the Caspian Sea. Stapf alludes to it as the Caspian Primrose. Harrison (*l.c.*, 75) has hybridised it successfully with several members of the Vernales.

P. vulgaris subsp. **Ingwerseniana** Harrison in *The Vasculum*, xvi, 5 (1930), and in *Trans. North. Nat. Union*, i, 48, 63, 66, 75 (1931).

The material on which the original diagnosis was based consisted of living plants collected by Mr. W. E. Th. Ingwersen "in early summer of 1929 on Mount Olympus, a day's march (2000–3000 ft.) above the Monastery of Dionysus, this being the nearest human habitation." The plant was sparingly grown in one or two gardens in this country before the war but at this date has almost vanished, if not completely so. Unfortunately its representation in any herbarium is meagre indeed. In the circumstances there is some difficulty in coming to a clear decision as to its status. In the description the more pertinent criteria are the white colour of the flower and the shape and pubescence of the leaf. From the single specimen available—if in such a case *ex uno disce omnes*—it may be said forthwith that it is equivalent neither to subsp. *balearica* nor to var. *atlantica* nor to var. *pulchella*—all with white flowers and all with a high degree of geographical isolation. Is *Ingwerseniana* similarly secluded? Hayek in *Prod. Fl. Penin. Balc.*, ii, 23 (1928) indicates that *P. vulgaris* is well distributed in the Balkans, including Greece, and that white forms occur. It seems unlikely that the white-flowered *Primula* on Mt. Olympus has been entirely overlooked in the past unless regarded as but a white form. On the other hand the foliage of *Ingwerseniana*—what is available—does not suggest *P. vulgaris*, and Harrison's experimental evidence must be noted: "Self-pollination of short-styled *P. Ingwerseniana*, in a small batch of seven plants, of which five have flowered, has given rise to three whites and two light mauves, thereby hinting that a dominant white is possible." Evidently more details are desirable as to the *Primula* population of Mt. Olympus. Meanwhile the plant in question is left *in statu quo ante bellum*!

P. vulgaris subsp. **Sibthorpii** (Hoffmannsegg) W. W. Sm. et Forrest in *Notes Roy. Bot. Gard. Edin.*, xvi, 42 (1928), and in *Journ. Roy. Hort. Soc.*, liv, 21 (1929); Harrison in *Trans. North. Nat. Union*, i, 48, 58, 59, 74 (1931). *P. Sibthorpii* Hoffmannsegg, *Preisverzeichnis*, 189 (1824); *Reichb. Fl. Germ. Excs.*, 402 (1830); Caruel in *Parlatore, Fl. Ital.*, viii, 610 (1889); *Wien. Ill. Gart.-Zeit.*, xxviii, 151, fig. 36 (1903); *Journ. Roy. Hort. Soc.*, xxxix, 167, 169, 171–172 (1913); *Bull. Acad. Sc. U.R.S.S.*, No. 2, 302 (1933). *P. acaulis* var. *Sibthorpii* Pax in *Engl. Bot. Jahrb.*, x, 181 (1889); Widmer, *Eur. Art. Prim.*,

127 (1891); Kusnetzow, Fl. Cauc. Crit., iv, 78 (1901). *P. acaulis* var. *rubra* Sibth. et Smith, Fl. Graec., ii, 70, t. 184 (1813); Ruprecht in Bull. Acad. St. Pétersburg, vi, 221 (1863); Halácsy, Consp. Fl. Graec., iii, 6 (1904); Pax in Engl. Pflanzenr. Primulaceae, 55 (1905); Farrer in Eng. Rock Gard., ii, 107, 182 (1928). *P. vulgaris* var. *rubra* (Sibth. and Smith) Lüdi in Hegi, Ill. Fl. Mittel-Eur., v, 1745 (1927); Stapf in Bot. Mag., t. 9166 (1929)—sub *P. vulgaris heterochroma*. *P. amoena* var. *acaulis* M. Bieb. Fl. Taur. Cauc., i, 138 (1808). *P. amoena* var. *Sibthorpii* C. Koch in Linnaea, xvii, 307 (1843). *P. acaulis* var. *iberica* G. F. Hoffmann, Hortus Mosquens., No. 2594 (1808)—nomen. *P. acaulis* var. *rosea* Boiss. Fl. Orient., iv, 24 (1879). ?*P. acaulis* var. *colorata* Ljungström in Bot. Centralbl., xxxv, 181 (1888). *P. acaulis* var. *fl. pleno carneo* Bot. Mag., t. 229 (1794). *P. grandiflora* var. *fl. purpureo* Duby in DC. Prodr., viii, 37 (1844). *P. grandiflora* var. *orientalis* C. Koch in sched. *P. Komarovi* Losin. in Bull. Acad. Sc. U.R.S.S., No. 2, 301 (1933). *P. Woronovi* Losin. (*l.c.*, 303). *P. abchasica* Sosnowsky in Trav. Inst. Bot. Tbilissi, ii, 231 (1938).

This subspecies is distributed in the Levant, including Thessaly, Constantinople, Crimea, Caucasus, Armenia, and N. Persia. It differs from the majority of its allies within the complex of *P. vulgaris* in the colour of the corolla, which may be purple, rose, lilac, white, red, or crimson. These shades predominate to the practical exclusion of yellow. In the European zone of *P. vulgaris* yellow is dominant, and other colours more or less fortuitous. But the nearest ally of subsp. *Sibthorpii* is the Caspian Primula, subsp. *heterochroma*, which has a wide colour range including yellow and white as well as shades of purple and azure-blue, and which is readily discriminated from the present plant by the white cobwebby-tomentum on the under-surface of the leaves.

Included in the synonymy are three plants recently published as species, all described from cultivated plants which had been obtained from the Caucasus and given a wide distribution in that region. It is strange that Kusnetzow (*l.c.*) in his exhaustive treatise on the Caucasian Primulas (based on his own explorations) failed to discriminate these, if the criteria are to any degree significant. From the diagnoses they do not appear to deviate from subsp. *Sibthorpii* in any essential.

Subsp. *Sibthorpii* has been known for over 250 years and has been in culture for almost as long. It has given rise to many garden

forms (Pax, *l.c.*, 56; Farrer, *l.c.*, 107). Its association with the Turkish capital is indicated by the citation (Sibth. and Smith, *l.c.*) of a synonym, *P. veris* β *constantinopolitana*, a varietal epithet which goes back at least to Tournefort. (It reappears with Goupil in Ann. Soc. Bot. Linn. Paris, iii, 247 (1825).)

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 — — *caulescens* (Koch) Miller Christy, 458.
vulgaris f. *caulescens* (Koch) Schinz et Thellung, 458.
vulgaris f. *colorata* Ljung., 457.
vulgaris subsp. *genuina* (Pax) Harrison, 454.
 — var. *genuina* (Pax) Beauverd, 454.
vulgaris subsp. *heterochroma* (Stapf) W. W. Sm. et Forrest, 461.
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vulgaris var. *hypoleuca* Beauverd, 459.
 — subsp. *Ingwerseniana* Harrison, 463.
 — f. *lactea* Ljung., 457.
 — f. *latiloba* Ljung., 457.
 — f. *longicalyx* Ljung., 457.
 — var. *obscura* Harrison, 459.
 — — *pulchella* (Heldr.) W. W. Sm. et Fletcher, 459.
vulgaris var. *purpurascens* Goup., 459.
 — — *purpurea* Maulny, 459.
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 — — *rubescens* Harrison, 460.
vulgaris var. *rubra* (Sibth. et Smith) Lüdi, 464.
vulgaris subsp. *Sibthorpii* (Hoffmannsegg) W. W. Sm. et Forrest, 463.
vulgaris subsp. *stenopetala* Harrison, 457.
vulgaris var. *truncata* Beauverd, 460.
 — f. *viridiflora* Druce, 460.
 — var. *viridimaculata* Harrison, 460.
 × *Wiesbaurii* Pax, 450.
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NOTES ON THE SCOTTISH RECORDS OF *CUSCUTA EUROPAEA*
LINN. By B. VERDCOURT.

(Read 12th June 1947.)

In the course of work in connection with the British Ecological Society's "Biological Flora of the British Isles", the writer was impressed with the dubious nature of the Scottish records of this plant. Opinions were obtained from several Scottish botanists and all were agreed that *Cuscuta europaea* had never been a plant indigenous to Scotland. The subject was pursued and the following notes may be of interest. With one exception, flowers from the herbarium specimens mentioned in this paper have been dissected and the epistaminal scales examined microscopically. Early botanists did not satisfactorily distinguish between the species of *Cuscuta* and hence early records are unreliable. Determinations of fresh material present no difficulty, but, in the case of herbarium material, the scales should always be mounted when there is any doubt. Really good illustrations of these scales indicating their variation within specific limits have yet to be made, but much help with identification may be obtained from the works of T. G. Yuncker (1, 2).

The Glasgow List (3) does not mention the plant. Watson (4) gives no records for Scotland, but notes that Roberts records the species from the counties of Dumfries, Lanark, Forfar, South Aberdeen, Edinburgh, and Roxburgh, and states that they are mostly errors. Druce (5) gives all of these counties, noting them as doubtful, and also gives an authentic record from Perth. Trail (6), summarising the status of *C. europaea* in Scotland, gives the counties mentioned above with the exception of South Aberdeen. The counties will now be considered in turn.

The Dumfries record was due to a misidentification of *C. Epilinum* Weihe, being based on specimens found on flax near Dumfries by C. N. Lloyd in 1837. These were incorrectly referred to *C. europaea* in Hooker and Arnott's "British Flora", which reference was subsequently copied in a county list (7). G. F. Scott Elliot (8) correctly refers to this record under *C. Epilinum* Weihe. The Lanarkshire record was a similar misidentification for *C. Epilinum*, specimens being recorded by the Rev. W. Patrick (9) under the name *C.*

europaea. G. Don's Forfar record is mentioned in Murray's "Northern Flora", but no specimens have been seen, and Trail states that the record requires confirmation. The South Aberdeen record refers to plants sent to Mr. Sowerby in 1797 by Mr. Alexander Smith of Aberdeen (see 10). The actual specimens still exist in the herbarium of Sir J. Edward Smith (Herb. Smith 242), which is kept at the Linnean Society of London. The label bears the following data: "Aberdeen, Mr. Alex. Smith, Sept. 1796", and the plant was in full fruit when collected. Microscopical preparations could not be made and the host is indeterminate, but the specimen is certainly *C. europaea*. Two sheets of *C. europaea* from the county of Edinburgh are in the herbarium of the Royal Botanic Garden, Edinburgh. One collected by John Knapp about 1834 is typical, but in the other, collected in potato fields at Edmonstone by Professor J. H. Balfour on 2nd September 1876, the scales are much larger, resembling those found in *C. Epithymum* (L.) Murr. *Cuscuta europaea* normally possesses two styles, but pistils bearing three are not uncommon. In the Edmonstone specimens, however, there is a tendency for the styles to be multiplied more than usual, some pistils bearing as many as five, though some of these are aborted. Four sheets from Roxburgh have been seen—one each in the herbaria of the British Museum (Nat. Hist.) and the South London Botanical Institute, and two in the Druce Herbarium at Oxford. It appears that all these sheets originated from the same gathering, but the labelling is most confused and the spelling varied. All would appear to have been collected at Blacklaw-Edge on *Vicia* sp., by A. Brotherston of Kelso, in August 1875. Of these four the South London Botanical Institute sheet is a form of *C. Epithymum* (L.) Murr, but incorrectly labelled *europaea*, and the British Museum and Druce sheets are forms of *europaea* with the scales more deeply cut than usual. The two sheets in the Druce Herbarium are both labelled *C. europaea* var. *nefrens* Fries. This is a variety in which the scales are supposed to be absent, but actually Fries's type bears quite normal-sized scales. A paper dealing with this point is shortly to be published elsewhere. The sheet in the British Museum Herbarium bears the imprint of the Botanical Record Club, and the reports of this Club (11) give this record in the new county record section. No specimen on which Roberts could have based his record has been seen, and in the absence of this the Blacklaw-Edge specimens should be accepted as the first authentic county record. The Perth record is given by F. B. White (12) as "once at Seggieden, Drummond Hay", but specimens could not be found in any of the

Scottish herbaria. A sheet in the General Herbarium at Kew is, however, undoubtedly the specimen referred to, since the label bears the date: "On Garden Hyssop, Seaggieden, Perth, H. M. Drummond Hay, Aug. 1874." . . . The specimen is fragmentary, but an examination was possible and it was confirmed as *C. europaea*, with the scales rather more deeply cut than usual.

It is therefore considered that there have been five occurrences of *C. europaea* in Scotland from the counties of South Aberdeen, Edinburgh, Roxburgh, and Perth. All were, however, almost certainly introductions. Statistical work on English records has shown that in the south at any rate the typical habitat is on nettles, by running water at altitudes of from 0 to 400 ft. No Scottish specimens have been seen from such a habitat. In the British Isles the species appears to be practically confined to the south, and reaches its maximum in the valleys of the rivers which flow towards the south and east coasts such as the Thames. It occurs as far north as 63° in Finland, but is rare. The mean summer temperature prevailing in Finland is, however, appreciably higher than that prevailing in Scotland, and it is probable that temperature is at least one of the factors preventing the spread of the species northward in the British Isles.

The writer wishes to thank Professor Graham, Mr. J. S. Whyte, and Dr. Taylor, in addition to the keepers of the various herbaria mentioned, for their very kind help.

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THE LEAF ANATOMY OF A NEW SPECIES OF *ARCHERIA* FROM
TASMANIA. By M. Y. ORR. (With Plate 10.)

(Read 12th June 1947.)

The subject of this brief communication is the peculiar and apparently unique construction of the leaves of a new species of *Archeria*, a member of the Epacrideae, which was found by Mr. H. F. Comber in the National Park, Tasmania, in 1929. A complete description of this species has not yet been published, but Mr. V. S. Summerhayes, of the Royal Botanic Gardens, Kew, has named it *Archeria Comberi* in honour of its discoverer.

Prior to this new record, three species of *Archeria* were known to occur in Tasmania and two in New Zealand, the species in each case being endemic in the country of its origin.

Archeria Comberi is said to be a low growing shrub, from 6 inches to 2 feet in height, and it differs outwardly from all other species of the genus in the smallness of its leaves, which are ovate in shape, sparsely serrated on the margin, and end in a minute, mucronate apex. The leaves are densely crowded on the branches, tending to become patent in the living state, when they are said to be of a green or purplish-red colour. The flowers are relatively large, of a pale pink hue, the sepals being small and the ovary glabrous, with a long style. According to the collector, the plants were growing in moist, well-drained situations near water.

It is in the internal structure of the leaves, however, that *Archeria Comberi* differs most markedly from all the other species. In the latter, taking *Archeria serpyllifolia* as an example (fig. 1), the leaves are pluricostate, and in transverse section the veins are seen to be situated close to the lower epidermis, from which they are separated by only a double layer of rounded cells. Each vascular bundle is partially encased in a semi-circular sheath of sclerenchyma, a feature which in varying degree is stated to be characteristic of the vascular system of most Epacrideae (1). The mesophyll above the vascular bundles consists mainly of palisade parenchyma, which is comparatively deep, but in the immediate vicinity of the bundles the tissue is less compact, and here and there intercellular spaces occur. Neither in this species nor in *Archeria eriocarpa* can it be said that the spongy parenchyma is well defined, although in the leaves of the

other species of *Archeria* this tissue is more prominent. It is generally conceded that a well-developed palisade tissue and a poorly organized spongy tissue are characteristic of xerophytes, and it is significant that in the leaves of *Archeria Comberi* the former tissue is not so well represented. The epidermis is composed of thick-walled cells with undulating lateral walls, a distinctive feature which, according to Simon (1), is common to the majority of the Epacrideae. The stomata are small in size, and are confined to the lower epidermis. They are superficial in position, and the air-shaft leading from the pore to the leaf interior is generally constricted, thus retarding the rate of transpiration. The amount of cuticle spread over the surface of the leaves varies somewhat according to the species. Apart from some minor differences, however, it can be said that the leaf-anatomy of the five old-established species of *Archeria* is essentially uniform throughout, and in the main is symptomatic of a xerophytic habit of life. There is certainly nothing phenomenal in the composition or the arrangement of the tissues in the leaves of any of the other five species of *Archeria*.

In the leaves of *Archeria Comberi* there is, however, a definite departure from the typical leaf-anatomy of the genus, for an entirely new kind of tissue is found here, interposed between the lower epidermis and the mesophyll, which is restricted to a narrow zone towards the upper side of the leaf. This tissue, the origin of which remains obscure, is composed of narrow elements, elongated vertically, and extending from the sparingly developed spongy parenchyma surrounding the vascular bundles to the single-layered hypodermis contiguous to the lower epidermis (fig. 2). These tubular elements are devoid of living contents, and have thin, unpitted walls, which tests have shown to be lignified. Some at least of these elements are forked at either end, and so are joined to two separate cells of the adjacent parenchyma. At the margin of the leaf, where there is less room for expansion, the cells of this particular tissue are curved and contorted, but towards the middle of the leaf these expand to their full extent, and may even become detached from the cells of the hypodermal layer with which they are normally connected (fig. 3). This happens inevitably when microscopic preparations are made from herbarium specimens. It is unfortunate that living material is unprocurable, since this species is not in cultivation, and the investigation of the leaf-anatomy had therefore to be carried out entirely on Comber's original specimens.

Thin transverse sections of the leaves give a false impression of the relative density of this peculiar tissue, for in bulk the elements

which comprise it are so closely packed that the air spaces between them are little more than capillaries. When a dry leaf is cut across, this tissue presents an appearance of a dense web of shining white hairs, suspended like a curtain from the narrow band of normal mesophyll at the upper side of the leaf.

So far as can be ascertained, having regard to the condition of the material available, the stomata, which are not numerous, and, as in the other species, are confined to the lower surface of the leaves, would not appear to be capable of performing their normal functions with efficiency in the living state. These organs are unusually superficial in position, and open into a narrow slit between the adjoining epidermal cells, the vertical walls of which bulge outwards into the air-shaft, thus diminishing the width and impeding the exchange of gasses as well as the exudation of water vapour. These constricted passages, leading inwards from the stomatal pore, do not in this case open into clearly defined air chambers, for at no point in the underlying parenchyma is there any indication of a break in its continuity. Normally, stomata communicate directly with the intercellular spaces of the spongy parenchyma, but in this case a tissue of a different category intervenes, and what effect this may have upon the vital processes of gas exchange and transpiration can be determined only when the purpose of the tissue becomes known. The unique character of this tissue, its singular construction and the position that it occupies in the leaves, presents an interesting problem in physiological plant-anatomy.

By the size and structure of their leaves, the other three Tasmanian species of *Archeria* clearly show adaptation to a xerophytic mode of life, and, although similar adaptive features are exhibited by the leaves of *Archeria Comberi*, the addition of this new tissue with its closely packed tubular cells, seems to indicate a possible reaction to some new factor in the immediate environment. Comber speaks of a moist habitat near water, but it is difficult to imagine how a tissue so constructed would better enable a supposedly xeromorphic species to cope with an increased water supply. The texture of the tissue is not suggestive of a device to accelerate transpiration, but is fitted rather to retard its flow by the creation of a saturated atmosphere in the capillaries, which are here the only way of communication between spongy parenchyma and stomata. If this were the case, this internal tissue of hair-like cells would then have an effect on the rate of transpiration similar to that produced by an external covering of pubescence. But as no such indumentum is found on the leaves of other species of the genus growing in drier

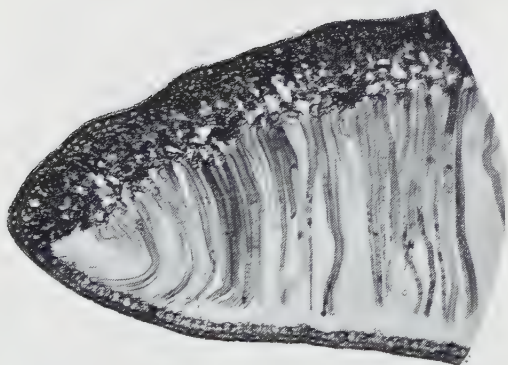
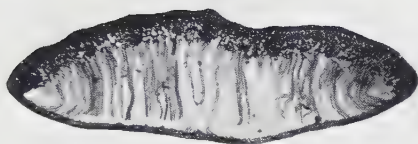
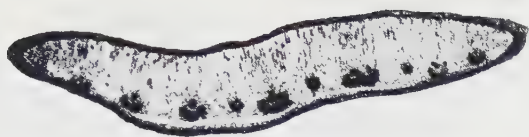


Fig. 1.—*Archeria serpyllifolia* Hook. f. (Comber, 1928). T. S. leaf, showing xeromorphic features. $\times 26$.

Fig. 2.—*Archeria Comberi* Summerhayes ined. (Comber, 1955). T.S. leaf, showing the "tubular tissue" interposed between the normal mesophyll and lower hypodermal layer. $\times 26$.

Fig. 3.—*Archeria Comberi*. T.S. leaf margin, showing curvature of the tubular elements, and their attachment to the cells of the spongy parenchyma. Their detachment from the hypodermis is accidental (see text). $\times 230$.

localities, why, therefore, should a species inhabiting a wetter situation be provided with an additional safeguard against excessive loss of water?

Other theories to account for the presence of this peculiar tissue in the leaves of *Archeria Comberi* suggest themselves, but none appears convincing, and all are open to criticism. Could the purpose of this tissue, comprising thin-walled elements possessing elasticity, yet lignified to withstand some degree of tension, be to allow of vertical expansion to deal with a possible seasonal increase in the volume of transpiration, at the same time obviating the danger of a consequent rupture of the dermal parenchyma? On the other hand, it seems unlikely, judging by its organization, that this tissue could act effectively as a water-storage organ in the event of a temporary decrease in the amount of water available for the plant.

The question of the origin of this tissue appears equally incapable of solution until its proper function is known. That it has arisen by modification of a pre-existing tissue of some other category seems improbable, since in the leaves of other species of *Archeria* there is no tissue which it could have replaced. Examination of the leaf primordia might conceivably throw light on this question of origin, but again lack of fresh material is an insuperable obstacle to further investigation on this point. Not until plants of this new species are accessible in the living state, and more detailed information is available regarding the conditions in which the plants grow in nature, will it be possible to arrive at a true explanation of the origin of this unique anatomical feature, and reveal the purpose it fulfils in the economy of this species.

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| May 1947. | HENRY, MRS. NORMAN, <i>Gladwyne, Pennsylvania, U.S.A.</i> |
| April 1938. | HU, H. H., D.Sc., <i>Professor of Botany, Fan Memorial Institute of Biology, 3 Wen Chin Street, Peiping, China.</i> |
| April 1938. | HUMBERT, Professor H., <i>Museum of Natural History, 55 Rue Cuvier, Paris.</i> |
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| Oct. 1935. | MİYABE, DR. KINGO, <i>Emeritus Professor of Botany, Hokkaido Imperial University, Sapporo, Hokkaido, Japan;—Corresponding Member, Dec. 1905.</i> |

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- May 1891. *Berwick, Thomas, *56 North Street, St. Andrews.*
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- Dec. 1886. *Bower, F. O., M.A., D.Sc., F.R.S., F.L.S., *The Old Deanery Hotel, Ripon.*
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- Dec. 1906. †Bryce, George, D.Sc., *c/o Union Bank of Scotland, 64 George Street, Edinburgh, 2.*
- Dec. 1935. Bryson, Arch. G., C.A., *20 Inverleith Place, Edinburgh, 4.*
- April 1926. Buchan, The Right Hon. the Earl of, *Almondell House, Mid-Calder.*
- Nov. 1922. Buchanan, E. M., *76 Warrender Park Road, Edinburgh, 10.*
- Dec. 1946. Burgess, J. S., B.Sc., *Science Dept., George Watson's Boys' College, Colinton Road, Edinburgh, 10.*
- Dec. 1921. Burns, W., C.I.E., D.Sc., F.R.S.E., *29 Craiglea Drive, Edinburgh, 10.*
- Dec. 1924. †Burt, Miss C. C., B.Sc., *Gogarburn Emergency Hospital, Edinburgh, 12.*
- Oct. 1947. Caird, F. M., B.Sc., *11 Melville Street, Perth.*
- Feb. 1941. Callen, Eric O., B.Sc., Ph.D., *Macdonald College, Quebec, Canada.*
- Oct. 1946. *Cameron, D., B.Sc., *Plant Breeding Station, Corstorphine, Edinburgh, 12.*
- Oct. 1925. Campbell, Mrs. Agnes, *53 Organgs Road, Edinburgh, 10.*
- Oct. 1937. Campbell, Miss May Sherwood, F.L.S., F.R.G.S., *83 Chatsworth Court, London, W. 8 (and Easter Tegarmuchd, by Aberfeldy, Perthshire).*
- Jan. 1947. Chakravarti, H. L., M.Sc., *Royal Botanic Garden, Edinburgh, 4.*
- Jan. 1935. Chen, Feng-hwai, *Lu Shan Botanical Garden, P.O. Box 4, Kuling, Kiukiang, China.*
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 Jan. 1947. Cockerham, George, B.Sc., Ph.D., *Plant Breeding Station, Craigs House, Corstorphine, Edinburgh, 12.*
 April 1913. *Cooper, R. E., *Royal Botanic Garden, Edinburgh, 4.*
 Jan. 1946. *Coutts, Wm. L., *11 Cadham Villas, Markinch, Fife.*
 Oct. 1930. Cowan, John M., M.A., D.Sc., *17 Inverleith Place, Edinburgh, 4.*
 April 1944. Cowan, William J., B.Sc., c/o Plant Protection Ltd., *Research Station, Fernhurst, Sussex.*
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 Jan. 1922. *Dales, Mrs. H., M.A., B.Sc., *Allora, Kensington Gardens, Knock, Belfast.*
 Jan. 1947. Das, M. C., M.Sc., *Royal Botanic Garden, Edinburgh, 4.*
 Oct. 1926. *Davey, V. E. M., B.Sc., Ph.D., *Plant Breeding Station, Corstorphine, Edinburgh, 12.*
 Dec. 1903. Davidson, J. Randolph, M.A., B.Sc., *25 Meadway Court, Golders Green, London, N.W. 11.*
 Dec. 1911. †Davidson, John, F.L.S., Associate Professor of Botany, *University of British Columbia, Vancouver, Canada.*
 Mar. 1946. Davis, P. H., c/o Miss Mason, *18 Brunton Terrace, Edinburgh, 7.*
 Dec. 1934. Dawson, J. L., B.Sc., *Four Winds, Charleston, Aberdeen.*
 Nov. 1927. *Dobson, Miss Margaret Gairns, *8 Polwarth Terrace, Edinburgh, 11.*
 Nov. 1919. *Downie, Miss D. G., B.Sc., Ph.D., *Department of Botany, Chanonry, Aberdeen.*
 Oct. 1944. *Duncan, Miss Ursula, *Parkhill, Arbroath.*
 Oct. 1936. Dundas, Lt.-Col., James C., D.S.O., *Ochertyre, Stirling.*
 April 1940. Dunn, Miss Mary D., B.Sc., Ph.D., *8 Whitehill Terrace, St. Andrews.*
 June 1940. *Easterbrook, Charles Cromhall, M.A., M.D., F.R.C.P.E., *Murrayfield Private Hotel, Edinburgh, 12.*
 Feb. 1917. †Eley, Charles, *East Bergholt Place, Suffolk.*
 Mar. 1932. Elphinstone, The Right Hon. Lady, *Carberry Tower, Musselburgh.*
 Dec. 1905. *Evans, W. Edgar, B.Sc., F.R.S.E., *38 Morningside Park, Edinburgh, 10.*
 Oct. 1947. Fairlie, Miss H., B.Sc., *Royal Botanic Garden, Edinburgh, 4.*
 Jan. 1935. Fang, Wen Pei, Ph.D., *Department of Biology, College of Science, National Szechuan University, Chengtu, Szechuan, China.*
 Dec. 1927. Fenton, E. Wyllie, M.A., D.Sc., F.L.S., *13 George Square, Edinburgh, 8.*
 Oct. 1943. Ferguson, Miss Emily A. K., B.Sc., *7 Comely Bank, Edinburgh, 4.*
 Oct. 1934. *Fleming, G. J., *Eastwood, Lauder.*
 Dec. 1934. *Fletcher, H. R., Ph.D., D.Sc., *Royal Botanic Garden, Edinburgh, 4.*
 Oct. 1928. Foister, Charles Edward, B.A., Ph.D., *The Croft, 9 Hillview Terrace, Corstorphine, Edinburgh, 12.*
 Oct. 1920. *Galloway, R. Angus, M.C., B.Sc., *65 Cluny Gardens, Edinburgh, 10.*
 Oct. 1947. *Galt, R. W. C., *20 Braid Farm Road, Edinburgh, 10.*
 Oct. 1947. Ganguly, A., B.Sc., *Scottish Society of Research in Plant-Breeding, Craigs House, Corstorphine, Edinburgh, 12.*
 Dec. 1920. †Garriock, John, M.A., B.Sc., *35 Craigmount Terrace, Corstorphine, Edinburgh, 12.*
 Feb. 1933. Gemmell, James W. S., M.A., B.Sc., *14 Headwell Road, Dunfermline.*
 May 1903. †Gilmore, Dr. Owen, L.R.C.P., L.R.C.S.E., *52 Chelsea Square, London, S.W. 3.*
 Oct. 1946. Gimingham, Charles H., B.A., *Botany Department, The University, Old Aberdeen.*
 Oct. 1936. *Gordon, Professor H. D., *Botany Department, Victoria University College, Wellington, New Zealand.*
 Oct. 1944. Gorrie, R. MacLagan, D.Sc., F.R.S.E., c/o Chief Conservator of Forests, *24 Cooper Road, Lahore, India.*
 Nov. 1921. *Graham, R. J. D., M.A., D.Sc., *Professor of Botany, The University, St. Andrews.*
 Feb. 1944. Gray, Miss Elizabeth, Ph.D., *North of Scotland College of Agriculture, 41½ Union Street, Aberdeen.*
 Jan. 1923. Gray, John H., M.A., B.Sc., *28 West Relugas Road, Edinburgh, 9.*
 Jan. 1926. Gregor, James W., Ph.D., D.Sc., F.L.S., *North Clermiston House, Barnton, Midlothian.*
 Mar. 1925. *Grieve, Miss Jean E., *The Latch, Marine Parade, North Berwick.*
 Dec. 1946. Haigh, J. C., B.Sc., Ph.D., A.R.C.S., *Scottish Plant Breeding Station, Boghall, Biggar Road, Edinburgh, 10.*

Date of Election.

- Nov. 1914. †Harley, Andrew, *Blinkbonny, Kirkcaldy.*
 Dec. 1923. †Harris, Mrs. K., B.Sc., *Oakleigh, Elm Road, Early, Reading.*
 April 1945. Harrison, Professor J. W. Heslop, D.Sc., F.R.S., *Department of Botany, King's College, Newcastle-upon-Tyne.*
 Dec. 1946. Harrison, J. Heslop, B.Sc., *Department of Botany, Queen's University, Belfast.*
 April 1910. *Harvey, Miss Elsie, *Kerala, Captain's Road, Liberton, Edinburgh, 9.*
 Oct. 1947. Hay, Miss M., *14 Warrender Park Road, Edinburgh, 4.*
 Oct. 1947. Hayes, S. F., B.Sc., *Royal Botanic Garden, Edinburgh, 4.*
 Mar. 1913. †Hayward Miss Ida M., F.L.S., *7 Abbotsford Road, Galashiels.*
 Oct. 1947. Heywood, V. H., *28 Craigleith Hill Crescent, Edinburgh, 4.*
 Dec. 1929. Heddle, R. G., M.A., B.Sc., *13 George Square, Edinburgh, 8.*
 Oct. 1926. †Home, Miss Logan, *Silverwells, Coldingham.*
 Dec. 1946. Irvine, F. R., D.Sc., F.L.S., *Zoology Department, Kings Buildings, West-Mains Road, Edinburgh, 9.*
 Jan. 1935. Jardine, Brig.-Gen. J. B., C.M.G., D.S.O., *Chesterknowes, by Selkirk.*
 Oct. 1931. *Jeffers, R. H., N.D.H., F.C.S., F.L.S., *42 Archery Road, Eltham, London, S.E. 9.*
 Dec. 1935. *Johnson, J. W. H., C.A., *12 Granby Road, Edinburgh, 9.*
 Dec. 1912. *Johnstone, James Todd, M.A., B.Sc., *36 Telford Road, Edinburgh, 4.*
 Dec. 1946. Johnstone, R. H., M.A., *726 Anniesland Road, Glasgow, W. 4.*
 Jan. 1913. *Kemp, Mrs. C. Norman, M.A., D.Sc., *Ivy Lodge, Laverockbank Road, Edinburgh, 5.*
 Oct. 1947. Kerr, A., B.Sc., *4 Fraser Crescent, Edinburgh, 5.*
 Dec. 1938. Kidd, Maurice G., B.L., W.S., *13 Melville Street, Edinburgh, 3.*
 Nov. 1924. *King, Miss C. A., *Osborne Nursery, Corstorphine Road, Edinburgh, 12.*
 Oct. 1921. *King, Miss Isabella M., B.Sc., *4 Cambridge Gardens, Edinburgh, 6.*
 Oct. 1947. Kirkcaldie, R. L., C.A., *104 Holyrood Road, Edinburgh, 8.*
 Jan. 1924. *Knox, Mrs. J., M.A., B.Sc., *43 Dalhousie Terrace, Edinburgh, 10.*
 Nov. 1921. *Laing, Ernest V., M.A., B.Sc., *13 Belvedere Street, Aberdeen.*
 Oct. 1935. Lamb, Ivan M., B.Sc., *Department of Botany, British Museum (Natural History), Cromwell Road, London, S.W. 7.*
 Dec. 1911. *Lamont, Miss Augusta, M.A., B.Sc., *Inverchaolain, Toward, Argyllshire.*
 Oct. 1935. Lauder, Thomas, *12 Adamswell Street, Glasgow, N.*
 Dec. 1922. *Lewis, Herbert M., B.Sc., *Westwood, Gresford, near Wrexham, Denbighshire.*
 Oct. 1947. Lyall, C. A., B.Sc., *Royal Botanic Garden, Edinburgh, 4.*
 Nov. 1922. †M'Call, David, B.Sc., Ph.C., *Dundee Technical College, Bell Street, Dundee.*
 Feb. 1933. Macdonald, James A., B.Sc., Ph.D., F.R.S.E., *Botany Department, The University, St. Andrews.*
 May 1936. *Macdonald, Miss Mary M., B.Sc., *11 Eyre Crescent, Edinburgh, 3.*
 Oct. 1947. McGehe, Miss T. M. R., B.Sc., N.D.D., *Scottish Society for Research in Plant Breeding, Craigs House, Corstorphine, Edinburgh, 12.*
 Dec. 1925. *M'Intosh, A. E. S., B.Sc., Ph.D., *Assistant Geneticist, Department of Science and Agriculture, Barbados, B.W.I.*
 Jan. 1946. Mackenzie, Robert, B.Sc., *9 Skirling Street, Shawlands, Glasgow, S. 1.*
 June 1945. MacLachlan, Mrs. S. H., *Leewood House, Dunblane.*
 Oct. 1947. M'Leod, Miss A. M., B.Sc., *Heriot-Watt College, Edinburgh, 1.*
 Dec. 1934. M'Rae, Wm., C.I.E., M.A., D.Sc., F.R.S.E., *Daramona, Gamekeeper's Road, Barnnton, Midlothian.*
 Dec. 1896. †Mahalanobis, Emeritus Professor S. C., B.Sc., F.R.S.E., *210 Cornwallis Street, Calcutta, 6.*
 Dec. 1934. Marindin, Mrs., *Fordel, Glenfarg, Perthshire.*
 Feb. 1936. Marindin, Miss Eve, *Fordel, Glenfarg, Perthshire.*
 Oct. 1914. *Martin, Miss Isa, M.A., *42 Craigmount Gardens, Edinburgh, 12.*
 Mar. 1913. *Matthews, James R., M.A., *Professor of Botany, The University, Old Aberdeen.*
 Dec. 1916. †Maxwell, Sir John Stirling, Bart., *Pollok, Pollokshaws, Glasgow.*
 April 1919. †Mills, A. E., *37 High Street, Keynsham, near Bristol.*
 May 1946. Molyneux, R. L. Newlyn, *15 Harewood Avenue, Morecambe, Lancs.*
 Oct. 1914. Montague, F. R., M.Ed., Ph.D., F.R.M.S., *Worksop College, Worksop, Notts.*
 Oct. 1944. Moore, Russell F., *475 5th Avenue, New York, 17, N.Y., U.S.A.*
 May 1947. Muirhead, Miss C. W., *Kelsick Moss House, Abbey Town, Carlisle.*
 Dec. 1943. Munro, Miss M. C. D., B.Sc., Ph.D., *Ministry of Agriculture and Fisheries, "Bracken Hill," North Road, Leigh Woods, Bristol, 8.*
 Dec. 1923. *Nelson, Alex., B.Sc., Ph.D., *Royal Botanic Garden, Edinburgh, 4.*
 Oct. 1943. Newton, Professor Lily, M.Sc., Ph.D., *University College of Wales, Aberystwyth.*
 Feb. 1944. *Noble, Mary, Ph.D., *19A Willowbrae Avenue, Edinburgh, 8.*
 Oct. 1946. Noronha, H. D., M.A., M.Sc., *Royal Botanic Garden, Edinburgh, 4.*
 Dec. 1907. *Orr, M. Y., F.R.S.E., *Royal Botanic Garden, Edinburgh, 4.*

Date of Election.

- Oct. 1937. *Paget, Lady, *Achnashellach, Ross-shire.*
 Oct. 1914. †Patton, Donald, M.A., B.Sc., Ph.D., 15 *Jordanhill Drive, Glasgow, W. 3*
 Oct. 1942. Pepall, Mrs. Ethel B. Le Roy, 43 *Dunvegan Road, Toronto, Ontario, Canada.*
 Dec. 1917. *Pike, J. Lyford, B.Sc., *Rosetta, 56 Kirkbrae, Liberton, Edinburgh, 9.*
 Jan. 1915. *Pinkerton, A. A., S.S.C., 10 *Castle Terrace, Edinburgh, 9.*
 Oct. 1937. Pollock, Sir J. Donald, Bart., O.B.E., LL.D., M.D., *Manor House, Boswall Road, Edinburgh, 5.*
 Dec. 1944. Preece, I. A., M.Sc., Ph.D., *Heriot-Watt College, Edinburgh, 1.*
 Feb. 1945. Preston, Rev. David, B.D., 1 *Wardie Road, Edinburgh, 5.*
 Oct. 1947. Raven, J. E., M.A., *Trinity College, Cambridge.*
 Dec. 1932. Redman, Miss A. W. H., B.Sc., 30 *Lomond Road, Edinburgh, 5.*
 Jan. 1946. *Rob, Miss C. M., *Catton Hall, Thirsk, Yorks.*
 Feb. 1926. Robb, William, N.D.A., *Craig's House, Corstorphine, Edinburgh, 12.*
 Mar. 1944. Roberts, J., c/o Smith, 4 *St. Bernard's Row, Edinburgh, 4.*
 Oct. 1946. Robertson, Mrs. Edith, B.Sc., *Botany Department, The University, Old Aberdeen.*
 Dec. 1944. Robertson, N. F., B.Sc., 61 *East Trinity Road, Edinburgh, 5.*
 Feb. 1942. Roger, J. G., B.Sc., *The Museum, The University, Manchester, 13.*
 Feb. 1938. Russell, Sir David, LL.D., F.L.S., *Roths, Markinch.*
 Oct. 1942. *Russell, Lady, *Roths, Markinch.*
 May 1945. *Salvesen, Harold Keith, M.A., F.R.S.E., *Inveralmond, Cramond, Midlothian.*
 Mar. 1935. *Sandilands, James, F.I.C., 102 *Westholmes Gardens, Musselburgh.*
 May 1926. †Sangster, Mrs. Iris, *Fullerswood Park, Mountain Side P.O., Jamaica.*
 Feb. 1932. *Scarlett, R. L., O.B.E., C.D.A., *Sweethope, Musselburgh.*
 Dec. 1887. †Scott, J. S., L.S.A., 69 *Clowes Street, West Gorton, Manchester.*
 Oct. 1947. Sheriffs, W. R., 27 *Mentone Terrace, Edinburgh, 9.*
 Feb. 1940. Simpson, John B., D.Sc., 39A *Fountainhall Road, Edinburgh, 9.*
 Oct. 1944. Simpson, N. Douglas, M.A., F.L.S., F.R.M.S., *Maesbury, 3 Cavendish Road, Bournemouth, Hants.*
 April 1940. *Sinclair, James, B.Sc., *Herbarium, Botanic Garden, Singapore.*
 Oct. 1939. Small, Professor James, D.Sc., F.R.S.E., 5 *Eden-a-Green, Randal Park, Belfast, N. Ireland.*
 Nov. 1914. *Smith, James L. S., M.A., B.Sc., 29 *Wardie Road, Edinburgh, 5.*
 Dec. 1917. †Smith, J. T., 68 *Tennant Street, Glasgow.*
 Oct. 1947. Smith, Miss M. McLean, B.Sc., *Institute of Seaweed Research, Inveresk Gate, Musselburgh.*
 Jan. 1902. *Smith, Professor Sir Wm. Wright, LL.D., F.R.S., *Regius Keeper, Royal Botanic Garden, Edinburgh, 4.*
 Nov. 1923. †Stern, Frederick, *Highdown, Goring-on-Sea.*
 Oct. 1923. †Stevenson, J. B., *Tower Court, Ascot.*
 Oct. 1914. †Stewart, Edward J. A., M.A., B.Sc., 8 *Manor Road, Jordanhill, Glasgow.*
 Dec. 1944. Stirling, Mrs. A. C., B.Sc., *Department of Bacteriology, College of Agriculture, 13 George Square, Edinburgh, 8.*
 May 1926. Sutherland, Lady, 3 *Eglinton Crescent, Edinburgh, 12.*
 Oct. 1926. *Taylor, George, D.Sc., F.R.S.E., *Department of Botany, British Museum (Natural History), Cromwell Road, London, S.W. 7.*
 Dec. 1922. †Taylor, George Crosbie, B.Sc., F.L.S., c/o R. H. Bath Ltd., *Wisbech, Cambs.*
 May 1923. †Taylor, James, M.A., B.Sc., *High School, Dalbeattie, Kirkcudbrightshire.*
 May 1923. †Taylor, R. A., B.Sc., Ph.D., *Department of Botany, University College, Dundee.*
 Oct. 1929. Terras, Mrs. Kate R., 4 *Orchardhead Road, Liberton, Edinburgh, 9.*
 Oct. 1932. Tetley, Miss U., M.Sc., *High Garth, Windermere, Westmorland.*
 April 1921. †Thompson, Professor J. MacLean, M.A., D.Sc., F.L.S., *Department of Botany, The University, Liverpool.*
 Oct. 1928. Thomson, John R., B.Sc., *Department of Agriculture, Dueim, Sudan.*
 Oct. 1926. Thomson, Miss Norah M'Nab, 8 *Belgrave Crescent, Edinburgh, 4.*
 Oct. 1943. Todd, James McArthur, B.Sc., 24 *Hawthornvale, Edinburgh, 6.*
 Mar. 1947. Walker, F. T., *Scottish Seaweed Research Association, Inveresk Gate, Musselburgh.*
 Mar. 1932. Walton, John, M.A., D.Sc., *Professor of Botany, The University, Glasgow.*
 Oct. 1940. Waterston, Miss Elspeth J., B.Sc., *Queen Anne Secondary School for Girls, Queen Anne Road, York.*
 Oct. 1939. Watson, E. V., B.Sc., Ph.D., 15 *Ilkley Road, Caversham, Reading.*
 Oct. 1918. †Watson, Harry, B.Sc., *Benmore Forest School, Dunoon, Argyll.*
 Oct. 1947. Watson, Miss P. J., M.A., *Scottish Society for Research in Plant Breeding, Craigs House, Corstorphine, Edinburgh, 12.*
 April 1921. *Watt, Miss Janet, 2 *Catherine Place, West, Edinburgh, 12.*
 April 1930. *Watt, Mrs. Menie, F.L.S., 24 *Cluny Drive, Edinburgh, 10.*

Date of Election.

- Oct. 1947. Watts, Miss J. P., B.Sc., *Edinburgh and East of Scotland College of Agriculture, 13 George Square, Edinburgh, 8.*
- Jan. 1947. Whinfield, Miss Barbara, M.Sc., *Department of Botany, The University Old Aberdeen.*
- Dec. 1947. Whiteside, Miss L. M. P., B.Sc., *18 Esplanade Terrace, Joppa, Portobello, Edinburgh.*
- Dec. 1930. *Whyte, James H., B.Sc., *Botany Department, University of Alberta, Edmonton, Canada.*
- Oct. 1935. Williamson, William, F.R.S.E., F.L.S., *47 St. Albans Road, Edinburgh, 9.*
- Feb. 1912. *Wilson, Malcolm, D.Sc., *Brentknoll, Kinnear Road, Edinburgh, 4.*
- Mar. 1909. *Wilson, Thos., Ph.C., *110 High Street, Burntisland.*
- Jan. 1923. *Younger, Harry Geo., *Belhaven House, Dunbar.*

ORDINARY MEMBERS.

- Feb. 1946. Angus, Andrew, *77 Moore-land Gardens, Addiewell, by West Calder, Midlothian.*
- Nov. 1932. Broadfoot, Miss J., B.Sc., *c/o Department of Agriculture and Lands, P.O. Box 387, Salisbury, Southern Rhodesia.*
- Nov. 1933. Cant, Miss Christine M., B.Sc., Ph.D., *26 Auchendoon Crescent, Seafield, Ayr.*
- Oct. 1936. Chisholm, Mrs., *4 Wardie Road, Edinburgh, 5.*
- Oct. 1946. Compton, J. C., *14 Magdala Crescent, Edinburgh, 12.*
- Dec. 1938. Crockett, Ian B., B.Sc., *17 Riverside Drive, Stirling.*
- Oct. 1931. Cunningham, Miss Mern, *6 Merchiston Bank Gardens, Edinburgh, 10.*
- Oct. 1943. Davidian, H. H., B.Sc., *55 York Place, Edinburgh, 1.*
- Jan. 1940. Dickson, Miss A. M., *Woodhouse, Dunscore, Dumfriesshire.*
- Oct. 1943. Donoghue, Mrs. J. M., B.Sc., *12 Bedford Terrace, Portobello, Edinburgh.*
- Nov. 1926. Drysdale, Miss D., *Royal Botanic Garden, Edinburgh, 4.*
- Dec. 1946. Duncan, Miss Catherine, *264 Easter Road, Edinburgh, 6.*
- Nov. 1927. Evans, Miss, *38 Morningside Park, Edinburgh, 10.*
- Dec. 1933. Fleming, Mrs. E. M., *10 Chester Street, Edinburgh, 3.*
- Dec. 1946. Graham, Miss Jane, *Darroch Hostel, E. Suffolk Road, Edinburgh, 9.*
- Nov. 1932. Hawkins, Miss K., B.Sc., *33 Queensferry Street, Edinburgh, 2.*
- Dec. 1945. Henderson, D. M., *c/o Penman, 22 Lauriston Place, Edinburgh, 3.*
- Dec. 1936. Kennedy, Miss Margaret C. L. S., B.Sc., *384 Ferry Road, Edinburgh, 5.*
- Oct. 1943. Kimpton, Miss M. S., B.Sc., *125 Hillhouse Road, Edinburgh, 4.*
- April 1925. M'Ilvenna, Wm. R., *14 Inverleith Place, Edinburgh, 4.*
- Nov. 1928. Murray, John, B.Sc., *Burnside, Broughton, Peeblesshire.*
- Nov. 1931. Orr, Harry B., B.Sc., Ph.D., *The Technical College, Canterbury, Kent.*
- Oct. 1944. Peill, Mrs. D. R. L., *54 Henderson Row, Edinburgh, 3.*
- April 1930. Robson, Thomas, *6 Kirkhill Road, Edinburgh, 9.*
- Feb. 1942. Rose, A. Jolly, *Careston, Kinnear Road, Edinburgh, 4.*
- Dec. 1945. Smith, C. E. D., *Cowan House, George Square, Edinburgh, 8.*
- April 1925. Smith, Thomas Arthur, *142 Greenbank Road, Edinburgh, 10.*
- Dec. 1930. Torbock, H. C., *Cross Rig Hall, Cliburn, Penrith.*
- Jan. 1937. Torrance, Miss Margaret, B.Sc., *10 Hermitage Drive, Edinburgh, 10.*
- Nov. 1931. Waterston, John M., B.Sc., *Senior Botanist, Department of Agriculture, Moon Plantation, Ibadan, Nigeria, B.W. Africa.*
- Mar. 1946. Watson, P., *57 Braid Avenue, Edinburgh, 10.*
- Dec. 1946. Wilson, Miss Sheila, *22 Ormidale Terrace, Edinburgh, 12.*

ASSOCIATE.

- Jan. 1906. Harrow, R. L., *Munstead Orchard, Godalming, Surrey.*
- Dec. 1945. Wilkie, David, *Royal Botanic Garden, Edinburgh, 4.*

LADY MEMBERS.

- April 1944. Anthony, Mrs., *120 Trinity Road, Edinburgh, 5.*
- Dec. 1944. Borthwick, Miss J. L., *3 Learmonth Park, Edinburgh, 4.*
- Dec. 1947. Burgess, Miss A. L., *30 Oxbang's Terrace, Edinburgh, 13.*
- Dec. 1926. Callender, Mrs. C. A., *5 Inverleith Place, Edinburgh, 4.*
- April 1944. Cameron, Mrs. C., *20 Cumlin Place, Edinburgh, 9.*

Date of Election.

Oct. 1943.	Cattanach, Miss M. M., 25 <i>Greenhill Gardens, Edinburgh</i> , 10.
May 1936.	Cowan, Mrs., B.A., 17 <i>Inverleith Place, Edinburgh</i> , 4.
Dec. 1947.	Darling, Mrs. W. N., 48 <i>Inverleith Place, Edinburgh</i> , 4.
Feb. 1937.	Fenton, Mrs. Wyllie, 16 <i>Wilton Road, Edinburgh</i> , 9.
May 1936.	Fleming, Miss Harriet, M.A., <i>Eastwood, Lauder</i> .
Mar. 1942.	Fletcher, Mrs., 26 <i>Bonnington Grove, Edinburgh</i> , 6.
April 1946.	Gregor, Mrs. Mary J. F., B.Sc., Ph.D., <i>North Clermiston House, Barnton, Midlothian</i> .
Oct. 1936.	Groves, Mrs. Anne M., 44 <i>Beauchamp Road, Liberton, Edinburgh</i> , 9.
Oct. 1936.	Gumley, Lady, 52 <i>Inverleith Row, Edinburgh</i> , 4.
Mar. 1946.	Haldane, Mrs. Janet M., <i>Cloan, Auchterarder, Perthshire</i> .
Dec. 1937.	MacArthur, Mrs. Enid Clark, 30 <i>Warriston Avenue, Edinburgh</i> , 4.
Dec. 1944.	MacColl, Mrs. M. H., 2 <i>High Street, Dysart, Fife</i> .
Oct. 1937.	Miller, Mrs. Hugh, 22 <i>Blacket Place, Edinburgh</i> , 9.
Feb. 1946.	Miller, Mrs. H. T., 30 <i>Queensferry Street, Edinburgh</i> , 2.
Dec. 1947.	Purves, Miss D., 60 <i>Orchard Road, Edinburgh</i> , 4.
Dec. 1947.	Simpson, Mrs. J. B., 39A <i>Fountainhall Road, Edinburgh</i> , 9.
Nov. 1926.	Smith, Lady, <i>Inverleith House, Edinburgh</i> , 4.
April 1944.	Stephen, Miss, 5 <i>Hope Street, St. Andrews</i> .
Feb. 1946.	Stott, Miss E. R., <i>Morven, Barnton, Midlothian</i> .

CORRESPONDING MEMBER.

Dec. 1905.	Mattirolo, Professor O., <i>R. Istituto Botanico, Torino</i> (120) <i>Italy</i> .
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PROCEEDINGS
OF THE
BOTANICAL SOCIETY OF EDINBURGH

SESSION CIX

OCTOBER 19, 1944.

Dr. E. WYLLIE FENTON, President, in the Chair.

The following Office-Bearers were elected for Session 1944-45.

PRESIDENT.

E. WYLLIE FENTON, M.A., D.Sc.

VICE-PRESIDENTS.

DAVID CLOUSTON, C.I.E., M.A., D.Sc.	WM. McRAE, C.I.E., M.A., D.Sc.
C. E. FOISTER, B.A., Ph.D.	Prof. J. R. MATTHEWS, M.A.

COUNCILLORS.

JOHN ANTHONY, M.C., M.A., B.Sc.	JAMES W. GREGOR, D.Sc.
W. BURNS, C.I.E., D.Sc.	Mrs J. KNOX, M.A., B.Sc.
JOHN DAVIDSON, B.Sc. (Econ.).	DAVID RUSSELL, LL.D.
W. EDGAR EVANS, B.Sc.	Prof. JOHN WALTON, M.A., D.Sc.
JOHN GARRIOCK, M.A., B.Sc.	MALCOLM WILSON, D.Sc.

Honorary Secretary—H. R. FLETCHER, D.Sc.

Foreign Secretary—Professor Sir WM. WRIGHT SMITH, M.A., LL.D.

Cryptogamic Secretary—C. E. FOISTER, B.A., Ph.D.

Treasurer—J. W. H. JOHNSON, C.A.

Assistant Secretary—J. T. JOHNSTONE, M.A., B.Sc.

Artist—R. M. ADAM, F.L.S.

Auditor—JOHN DAVIDSON, B.Sc. (Econ.).

The TREASURER, Mr. J. W. H. JOHNSON, C.A., submitted the following Statement of Accounts for Session 1943-44:—

INCOME.

Annual Subscriptions for 1943-1944	£52 5 0
Do. Arrears	29 0 0
Transactions sold	8 17 0
Interest on Funds Invested and in Bank	14 18 8
Subscriptions to Publications Fund	31 11 0
Income from Botanical Society Trust Fund	11 0 4
Income Tax recovered	14 15 0
	<u>£162 7 0</u>

EXPENDITURE.

Printing <i>Transactions</i> for Session 1942-1943	£145 10 0
Printing and Postage of Notices for Meetings	29 16 0
Expenses of Lectures	1 1 0
Teas	6 2 0
Stationery, Postages, etc.	4 4 7
Fire Insurance on Books	0 5 0
Honorarium to Treasurer	3 3 0
	<u>£190 1 7</u>
Excess of Expenditure	<u>£27 14 7</u>

STATE OF FUNDS.

Life Members' Fund.

Balance of Fund at close of Session 1942-1943	£489 0 7
Add—Life Composition received	35 4 0
Balance as at close of Session	<u>£524 4 7</u>

Ordinary Fund.

Balance of Fund at close of Session 1942-1943	£249 2 4
Less—Decrease during Session 1943-1944	27 14 7
Balance as at close of Session, subject to expense of printing <i>Transactions</i>	<u>221 7 9</u>
Total Funds	<u>£745 12 4</u>
Being :—£200 $3\frac{1}{2}\%$ War Stock, at cost	£194 18 3
£250 London & North Eastern Railway Co. 3% Debenture Stock at cost	216 18 6
£100 3% Defence Bonds	100 0 0
Sums on Deposit Receipt with Union Bank of Scotland, Ltd.	150 0 0
Sum in Current Account with do.	89 5 7
	<u>£751 2 4</u>
Less—Subscriptions received in advance	5 10 0
As above	<u>£745 12 4</u>

Note.—Subscriptions in arrear, considered recoverable, 1942-43, £7.
1943-44, £20.

EDINBURGH, 9th October 1944.—I hereby certify that I have audited the Accounts of the Treasurer of the Botanical Society of Edinburgh for Session 1943-1944, and have found them correct. I have also checked the foregoing Abstract, and find it correct. I have seen the securities for the invested funds and have found them in order.

JOHN DAVIDSON, *Auditor.*

BOTANICAL SOCIETY TRUST FUND.

 SESSION 1943-1944.

INCOME.

Interest on Funds invested	£11 0 4
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EXPENDITURE.

To Publications Fund	£11 0 4
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EDINBURGH, 26th June 1944.—I certify that I have examined the above account and relative vouchers of the Edinburgh Botanical Society Trust Fund, and found the same to be correct.

ALEX. ARNOTT.

Miss URSULA DUNCAN, Dr. MACLAGAN GORRIE, Dr. F. R. MONTAGUE, Capt. RUSSELL F. MOORE, and Mr. N. DOUGLAS SIMPSON were elected Ordinary Fellows.

Miss AUDREY M. SUTCLIFFE was elected an Ordinary Member.

Mr. R. M. ADAM read a paper, "National Parks for Scotland—A Naturalist's Choice," which he illustrated with a large number of lantern slides.

 NOVEMBER 23, 1944.

Dr. E. WYLLIE FENTON, President, in the Chair.

Dr. R. MACLAGAN GORRIE read a paper on Progress in Soil Erosion Control in India, which he illustrated with a number of lantern slides.

 DECEMBER 14, 1944.

Dr. E. WYLLIE FENTON, President, in the Chair.

Mrs. A. C. STIRLING, Dr. I. A. PREECE, and Mr. N. F. ROBERTSON were elected Ordinary Fellows.

Miss M. H. ORR and Miss J. L. BORTHWICK were elected Lady Members.

Dr. W. BURNS read a paper dealing with the Story of Plant Breeding in India and illustrated it with numerous lantern slides.

JANUARY 18, 1945.

Dr. E. WYLLIE FENTON, President, in the Chair.

Lt.-Col. F. R. S. BALFOUR read a paper on Archibald Menzies and his Exploration with Vancouver of the N.W. American Coast. As the lecturer himself had travelled over some of the same mountain trails he was able to show lantern slides of some of Menzies' discoveries in their native habitat.

FEBRUARY 15, 1945.

Dr. E. WYLLIE FENTON, President, in the Chair.

The following motion on Alteration of Laws, moved by Dr. E. WYLLIE FENTON and seconded by Mr. JOHN DAVIDSON, was unanimously agreed to:—

Chapter IV. Admission of Members.

That paragraph 3 of Section II be altered to read:—

Ordinary Fellows may at any time compound for their annual contributions by payment of Ten Guineas, less an amount equal to one-third of the annual subscriptions previously paid. They shall be entitled to receive the *Transactions* yearly as published.

The PRESIDENT announced the death on 2nd February of Lt.-Col. F. R. S. BALFOUR, a Fellow since 1908, who was the lecturer at the previous meeting.

Dr. E. WYLLIE FENTON delivered his Presidential Address (see p. 213).

MARCH 15, 1945.

Dr. E. WYLLIE FENTON, President, in the Chair.

The PRESIDENT announced the death of Miss EDITH MERCER, an Ordinary Fellow since 1925.

Dr. W. BLACK read a paper on Wild Species and Cultivated Varieties of Potatoes, which he illustrated with numerous lantern slides and specimens of many of the varieties.

APRIL 19, 1945

Dr. E. WYLLIE FENTON, President, in the Chair.

Professor J. W. HESLOP HARRISON, Dr. W. A. CLARK, and Mr. A. GODFREY CRUFT were elected Ordinary Fellows.

The PRESIDENT announced the death of Mr. C. E. PARKINSON on the 25th March. He joined the Society in March 1941 after his retirement from the Burma Forest Service.

Capt. E. G. BIRD showed a film (partly in colour) illustrating the natural history of Greenland. An interesting discussion followed in which, among others, Miss HUTCHINSON and Mr. KAARE RODAHL took part.

MAY 17, 1945.

Dr. E. WYLLIE FENTON, President, in the Chair.

Mr. HAROLD KEITH SALVESEN was elected an Ordinary Fellow.

The PRESIDENT announced the death of Emeritus Professor WILLIAM TRELEASE, who had been an Honorary Fellow since 1902.

On behalf of Mr. KAARE RODAHL a paper was read on Vitamin B1 Content of Arctic Plants and Animal Tissue (see p. 244).

A paper by Dr. W. WATSON, "Notes on Lichens in the Herbarium of the Royal Botanic Garden, Edinburgh. IV.," was read by title (see p. 233).

JUNE 14, 1945.

Dr. E. WYLLIE FENTON, President, in the Chair.

Dr. S. H. MACLACHLAN was elected an Ordinary Fellow.

The death of Mr. J. RUSSELL-MURRAY of Montreal was announced. He had been a Fellow since 1889.

Mr. R. E. COOPER read a paper, "Some Observations on Giant Lobelias."

A paper by Dr. W. A. CLARK and Mr. R. B. COOKE on the Moss Flora of the Island of Rhum (see p. 252) and another by Professor J. W. HESLOP HARRISON on Sedges new to, or rare in, the British Isles from the Inner and Outer Hebrides (see p. 271), were read by title.

There was shown a short film taken by C. S. GARNETT, Esq., in Morocco, showing principally the Argan Tree (*Argania Sideroxylon*) being grazed by goats. A number of Sedges from the Hebrides were exhibited on behalf of Professor J. W. HESLOP HARRISON. Flowering plants of *Arundinaria falcata* and *Bambusa variegata*, also growing plants of *Lobelia Gibberoa* and *L. Elgonensis* (not in flower), were exhibited from the Royal Botanic Garden.

PROCEEDINGS
OF THE
BOTANICAL SOCIETY OF EDINBURGH

SESSION CX

OCTOBER 18, 1945.

Dr. E. WYLLIE FENTON, President, in the Chair.

The following Office-Bearers were elected for Session 1945-46:

PRESIDENT.

JAMES W. GREGOR, D.Sc.

VICE-PRESIDENTS.

C. E. FOISTER, B.A., Ph.D.
Prof. J. R. MATTHEWS, M.A.

DAVID RUSSELL, LL.D.
MALCOLM WILSON, D.Sc.

COUNCILLORS.

JOHN ANTHONY, M.C., M.A., B.Sc.
WILLIAM BLACK, Ph.D.
W. BURNS, C.I.E., D.Sc.
DAVID CLOUSTON, C.I.E., M.A., D.Sc.
JOHN DAVIDSON, B.Sc. (Econ.).

E. WYLLIE FENTON, M.A., D.Sc.
JOHN GARRIOCK, M.A., B.Sc.
MRS J. KNOX, M.A., B.Sc.
WM. McRAE, C.I.E., M.A., D.Sc.
Prof. JOHN WALTON, M.A., D.Sc.

Honorary Secretary—H. R. FLETCHER, D.Sc.

Foreign Secretary—Professor Sir WM. WRIGHT SMITH, M.A., LL.D., F.R.S.

Cryptogamic Secretary—C. E. FOISTER, B.A., Ph.D.

Treasurer—J. W. H. JOHNSON, C.A.

Assistant Secretary—J. T. JOHNSTONE, M.A., B.Sc.

Artist—R. M. ADAM, F.L.S.

Auditor—JOHN DAVIDSON, B.Sc.(Econ.).

The TREASURER, Mr. J. W. H. JOHNSON, C.A., submitted the following Statement of Accounts for Session 1944-45:—

INCOME.		
Annual Subscriptions for 1944-1945	£45	0 0
Do. Arrears	11	5 0
Transactions sold	14	12 6
Interest on Funds Invested and in Bank	14	10 10
Subscriptions to Publications Fund	48	13 0
Income from Botanical Society Trust Fund	11	0 6
Income Tax recovered	14	15 0
	<u>£159</u>	<u>16 10</u>
EXPENDITURE.		
Printing <i>Transactions</i> for Session 1943-1944	£213	15 0
Printing and Postage of Notices for Meetings	36	9 4
Teas	6	18 2
Stationery, Postages, etc.	5	19 5
Fire Insurance on Books	0	5 0
Honorarium to Treasurer	3	3 0
	<u>£266</u>	<u>9 11</u>
Excess of Expenditure	<u>£106</u>	<u>13 1</u>

STATE OF FUNDS.

Life Members' Fund.

Balance of Fund at close of Session 1943-1944	£524	4 7
Add—Life Composition received	57	7 0
Balance as at close of Session	£581	11 7

Ordinary Fund.

Balance of Fund at close of Session 1943-1944	£221	7 9
Less—Decrease during Session 1944-1945	106	13 1
Balance as at close of Session, subject to expense of printing <i>Transactions</i>	114	14 8
Total Funds	£696	6 3
Being:—£200 3½% War Stock, at cost	£194	18 3
£250 London & North Eastern Railway Co. 3% Debenture Stock at cost	216	18 6
£100 3% Defence Bonds	100	0 0
Sums on Deposit Receipt with Union Bank of Scotland, Ltd.	150	0 0
Sum in Current Account with do.	41	9 6
	<u>£703</u>	<u>6 3</u>
Less—Subscriptions received in advance and in suspense	7	0 0
As above	<u>£696</u>	<u>6 3</u>

Note.—Subscriptions in arrear, considered recoverable, £30.

EDINBURGH, 1st October 1945.—I hereby certify that I have audited the Accounts of the Treasurer of the Botanical Society of Edinburgh for Session 1944-1945, and have found them correct. I have also checked the foregoing Abstract, and find it correct. I have seen the securities for the invested funds and have found them in order.

JOHN DAVIDSON, Auditor.

BOTANICAL SOCIETY TRUST FUND.

 SESSION 1944-1945.

INCOME.

Interest on Funds invested	£11 0 6
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EXPENDITURE.

To Publications Fund	£11 0 6
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EDINBURGH, 6th July 1945.—I certify that I have examined the above account and relative vouchers of the Edinburgh Botanical Society Trust Fund, and found the same to be correct.

ALEX. ARNOTT.

Dr. KATHLEEN B. BLACKBURN was elected an Ordinary Fellow.

Dr. J. M. COWAN gave an account of his war-time work in the woods of the Western Highlands which he illustrated with a number of lantern slides.

 NOVEMBER 15, 1945.

Dr. J. W. GREGOR, President, in the Chair.

Dr. W. A. CLARK read a paper on Plant Hunting in the Hebrides and illustrated it with a number of lantern slides.

 DECEMBER 13, 1945.

Dr. J. W. GREGOR, President, in the Chair.

The following Honorary Fellows were elected: British, Mr. J. L. S. GILMOUR, Dr. S. C. HARLAND, Dr. JOHN HUTCHINSON, and Dr. F. E. WEISS; Foreign, Dr. L. H. BAILEY, Dr. A. J. EAMES, Dr. G. ERDTMAN, Dr. E. D. MERRILL, and Dr. FRANS VERDOORN.

Mr. DAVID WILKIE was elected an Associate.

Mr. WILLIAM L. COUTTS was elected an Ordinary Fellow.

Miss ROSEMARY ANGEL, Miss M. CLARK, Miss H. FAIRLIE, Mr. D. M. HENDERSON, Mr. A. KERR, and Mr. C. E. D. SMITH were elected Ordinary Members.

The President intimated the death of Professor N. I. VAVILOFF who had been an Honorary Fellow since 1934, and also the death of Dr. JAMES WATT who had been an Ordinary Fellow since 1925.

Dr. H. R. FLETCHER read a paper on New Approaches towards a Classification of the Angiosperms.

JANUARY 17, 1946.

Dr. J. W. GREGOR, President, in the Chair.

Mr. C. C. V. BATTS, Mr. RICHARD CUMMING, Mr. ROBERT MACKECHNIE, and Miss C. M. ROB were elected Ordinary Fellows.

Dr. S. WILLIAMS read a paper on Experimental Morphology, which he illustrated with lantern slides.

FEBRUARY 14, 1946.

Dr. J. W. GREGOR, President, in the Chair.

Mrs. H. T. MILLER and Miss E. R. STOTT were elected Lady Members. Mr. ANDREW ANGUS was elected an Ordinary Member.

Mrs. E. CONWAY read a paper on Agar-Agar and its Supply, which she illustrated with specimens, preparations, and some lantern slides.

MARCH 14, 1946.

Dr. J. W. GREGOR, President, in the Chair.

Mr. P. H. DAVIS was elected an Ordinary Fellow.

Mrs. JANET M. HALDANE was elected a Lady Member.

Mr. V. HEYWOOD and Mr. P. WATSON were elected Ordinary Members.

Mr. R. M. ADAM gave an account of some Scottish Seaweeds, which he illustrated with many lantern slides.

Dr. E. G. V. PERCIVAL gave an account of a number of products made from Scottish seaweeds, which he illustrated with a number of experiments.

APRIL 18, 1946.

Dr. J. W. GREGOR, President, in the Chair.

Dr. MARY J. F. GREGOR was elected a Lady Member.

Professor S. J. WATSON read a paper on the Conservation of Grass and other Green Crops for feeding to animals, and showed a number of lantern slides.

MAY 16, 1946.

Dr. J. W. GREGOR, President, in the Chair.

Mr. R. L. MOLYNEUX was elected an Ordinary Fellow.

The PRESIDENT drew the attention of Fellows to the proposed revised Rules of the Society which had been circulated with the

Billet for the meeting, and to the notice that any proposed amendments be sent to the Honorary Secretary by 28th May 1946.

Dr. GEORGE BOND read a paper on Dehydrated Foods and exhibited a number of specimens to illustrate it.

Two papers by E. V. WATSON were read by title, viz. "Observations on the Mosses of Wester Ross" (see p. 279) and "A Note on the Mountain-top Detritus Formation as seen on Beinn Damh, Wester Ross."

Dr. J. W. GREGOR exhibited two forms, of different habit, of *Saxifraga caespitosa* which he had raised from seed gathered on Ben Nevis. One of the forms was apetalous.

JUNE 13, 1946.

Dr. MALCOLM WILSON, Vice-President, in the Chair.

The proposed new Rules of the Society (with two minor amendments recommended by Council) were unanimously agreed to (a copy is at the end of this part).

Dr. E. V. WATSON read a paper "Notes on some interesting British Mosses" and exhibited a number of specimens.

The following papers were read by title: A List of the Bryophytes of Berwickshire (V.C. 81), by J. B. DUNCAN (see p. 288). The Genus *Primula*: Sections *Cuneifolia* Balf. f., *Floribunda* Pax, *Parryi* W. W. Sm., by W. WRIGHT SMITH and H. R. FLETCHER. Corm and Bulb Formation in Plants, with special reference to the Gramineae, by Dr. W. BURNS (see p. 316). An Account of $\times$ *Potamogeton suecicus* Richt. in Yorkshire and the Tweed, by J. E. DANDY and G. TAYLOR (see p. 348). A Comparative Account of the Structure of *Potamogeton filiformis* Pers. and *P. pectinatus* Linn. in Relation to the Identity of a Supposed Hybrid of these Species, by Miss H. MARGARET BANCE (see p. 361).

The following plants in flower were shown from the Royal Botanic Garden: *Calceolaria bicolor* Ruiz et Pavon; *Cuscuta Gronovii* Willd. (on *Chrysanthemum* sp.); *C. maritima* Makino (on *Artemisia* sp.); *Disa tripetaloides* N.E. Br.; *Drosera capensis* Linn.; *Erica Cavendishiana* Paxt.; *Gesnera allagophylla* Mart. and *Phaius Wallichii* Lindl.

PROCEEDINGS
OF THE
BOTANICAL SOCIETY OF EDINBURGH

SESSION CXI

OCTOBER 24, 1946.

Dr. J. W. GREGOR, President, in the Chair.

The following Office-Bearers were elected for Session 1946-47:

PRESIDENT.

JAMES W. GREGOR, D.Sc.

VICE-PRESIDENTS.

JOHN ANTHONY, M.C., M.A., B.Sc.	Sir DAVID RUSSELL, LL.D.
Mrs. J. KNOX, M.A., B.Sc.	MALCOLM WILSON, D.Sc.

COUNCILLORS.

WILLIAM BLACK, Ph.D.	JOHN GARRIOCK, M.A., B.Sc.
W. BURNS, C.I.E., D.Sc.	J. T. JOHNSTONE, M.A., B.Sc.
DAVID CLOUSTON, C.I.E., M.A., D.Sc.	WM. M'RAE, C.I.E., M.A., D.Sc.
MISS URSULA DUNCAN.	Professor J. R. MATTHEWS, M.A.
E. WYLLIE FENTON, M.A., D.Sc.	J. B. SIMPSON, D.Sc.

Honorary Secretary—H. R. FLETCHER, D.Sc.

Foreign Secretary—Professor Sir WM. WRIGHT SMITH, M.A., LL.D., F.R.S.

Cryptogamic Secretary—C. E. FOISTER, B.A., Ph.D.

Treasurer—J. W. H. JOHNSON, C.A.

Assistant Secretary—J. SINCLAIR, B.Sc.

Artist—R. M. ADAM, F.L.S.

Auditor—CHARLES A. SCOTT, C.A.

The TREASURER, Mr. J. W. H. JOHNSON, C.A., submitted the following Statement of Accounts for Session 1945-46—:

INCOME.

Annual Subscriptions for 1945-1946	£42 0 0
Do. Arrears	16 0 0
Transactions sold	8 6 3
Interest on Funds Invested and in Bank	15 6 2
Subscriptions to Publications Fund	25 7 6
Income from Botanical Society Trust Fund	11 11 2
Income Tax recovered	14 15 0
Donation	115 0 0
	<u>£248 6 1</u>

EXPENDITURE.

Printing <i>Transactions</i> for Session 1944-1945	£87 15 0
Printing and Postage of Notices for Meetings	46 17 6
Teas	5 9 11
Stationery, Postages, etc.	9 7 10
Fire Insurance on Books	0 5 0
Honorarium to Treasurer	3 3 0
	<u>£152 18 3</u>
Excess of Income	<u>£95 7 10</u>

STATE OF FUNDS.

Life Members' Fund.

Balance of Fund at close of Session 1944-1945	£581 11 7
Add—Life Compositions received	97 17 0
Balance as at close of Session	<u>£679 8 7</u>

Ordinary Fund.

Balance of Fund at close of Session 1944-1945	£114 14 8
Add—Increase during Session 1945-1946	95 7 10
Balance as at close of Session, subject to expense of printing <i>Transactions</i>	<u>210 2 6</u>
Total Funds	<u>£889 11 1</u>

Being:—£200 3½% War Stock, at cost	£194 18 3
£250 London & North Eastern Railway Co. 3% Debenture Stock at cost	216 18 6
£200 3% Defence Bonds	200 0 0
Sums on Deposit Receipt with Union Bank of Scotland, Ltd.	150 0 0
Sum in Current Account with do.	131 19 4
	<u>£893 16 1</u>

Less—Subscriptions received in advance and in suspense

4 5 0
<u>As above</u>

£889 11 1

Note.—Subscriptions in arrear, considered recoverable, £30.

EDINBURGH, 7th October 1946.—I hereby certify that I have audited the Accounts of the Treasurer of the Botanical Society of Edinburgh for Session 1945-1946, and have found them correct. I have also checked the foregoing Abstract, and find it correct. I have seen the securities for the invested funds and have found them in order.

CHARLES A. SCOTT, C.A., Auditor.

BOTANICAL SOCIETY TRUST FUND.

 SESSION 1945-1946.

INCOME.

Interest on Funds invested	<u>£11 11 2</u>
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EXPENDITURE.

To Publications Fund	<u>£11 11 2</u>
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EDINBURGH, 3rd July 1946.—I certify that I have examined the above account and relative vouchers of the Edinburgh Botanical Society Trust Fund, and found the same to be correct.

ALEX. ARNOTT.

Mr. W. BLYTH, Mr. D. CAMERON, Mr. C. H. GIMMINGHAM, Mr. H. D. NORONHA, and Mrs. E. ROBERTSON were elected Ordinary Fellows.

Mr. J. C. COMPTON, Mr. ROBERT W. C. GALT, and Miss MURIEL J. HAY were elected Ordinary Members.

Mr. P. H. DAVIS read a paper on Plant Life in the Near East, which he illustrated with lantern slides and herbarium specimens.

NOVEMBER 21, 1946.

Dr. J. W. GREGOR, President, in the Chair.

The PRESIDENT referred to the deaths of two Fellows: Dr. J. J. BLACKIE, who joined the Society in April 1926 and was a Councillor for several years; and Mr. J. DAVIDSON, who joined in February 1940 and acted on the Council and as Auditor.

Dr. FOISTER read the Report of the Meeting and Foray of the Cryptogamic Section of the Society, held on 4th and 5th October 1946, at Peebles. (See p. 392.)

Dr. NOBLE referred to and exhibited J. E. SMITH's "Compendium Florae Britannicae" (1816), with MS. notes by R. K. GREVILLE, which she gifted to the Society.

Dr. BURNS read a paper, "Some Thoughts on Evolution," which he illustrated with a number of drawings and botanical specimens.

DECEMBER 12, 1946.

Dr. J. W. GREGOR, President, in the Chair.

Sir J. D. ANDERSON, Mr. J. S. BURGESS, Dr. J. C. HAIGH, Mr. J. HESLOP HARRISON, Dr. F. R. IRVINE, and Mr. R. H. JOHNSTONE were elected Ordinary Fellows.

Miss CATHRINE DUNCAN, Miss JANE GRAHAM, and Miss SHEILA WILSON were elected Ordinary Members.

The PRESIDENT delivered his Address on "Some Reflections on Intra-Specific Ecological Variation and its Classification," which he illustrated with a number of coloured lantern slides. (See p. 377.)

JANUARY 23, 1947.

Dr. J. W. GREGOR, President, in the Chair.

Mr. H. L. CHAKRAVARTI, Dr. G. COCKERHAM, Mr. M. C. DAS, and Miss BARBARA WHINFIELD were elected Ordinary Fellows.

Mr. P. W. GUNN read a paper entitled "From St. Abbs to Ben Lomond: a Naturalist surveys the Forth Area," which he illustrated with lantern slides.

FEBRUARY 20, 1947.

Dr. WYLLIE FENTON in the Chair.

Dr. K. B. BLACKBURN read a paper entitled "History of the Vegetation of the Western Isles as told by Peats," which she illustrated with lantern slides.

MARCH 13, 1947.

Dr. J. W. GREGOR, President, in the Chair.

Miss E. CLAY and Mr. F. T. WALKER were elected Ordinary Fellows.

The PRESIDENT, on behalf of the Society, presented Mr. J. T. JOHNSTONE with a cheque and referred to his long term of service as Assistant Secretary.

The PRESIDENT referred to the death of the oldest Fellow of the Society, The Honourable Mr. JUSTICE RIDDELL, who was elected in April 1877.

Dr. J. B. SIMPSON read a paper entitled "Tertiary Pollen Grains," which he illustrated with lantern slides.

APRIL 17, 1947.

Dr. WYLLIE FENTON in the Chair.

The CHAIRMAN referred to the deaths of Mr. WM. YOUNG, a past President; MATTHEW V. HUNTER, Ph.C., Ph.D., a Fellow; and R. STEWART MACDOUGALL, D.Sc., LL.D., a past President.

Dr. STEWART MACDOUGALL bequeathed £100 to the Society.

Dr. MARY NOBLE read a paper on Early Mycological Work in Scotland, which she illustrated with lantern slides.

MAY 15, 1947.

Dr. J. W. GREGOR, President, in the Chair.

Mrs. NORMAN HENRY was elected an Honorary Foreign Fellow.

Miss C. W. MUIRHEAD was elected an Ordinary Fellow.

Mr. J. M'CLOY read a paper on Sugar Beet in Scotland, which he illustrated with a number of lantern slides.

The following papers were read by title:—

1. "The Potamogetons of the Western Isles, with some Account of the General Natural History of the Group." By J. W. HESLOP HARRISON.
 2. "New and Interesting British Records of Potamogeton." By J. E. DANDY and G. TAYLOR.
 3. "The Genus *Primula*: Section *Vernales* Pax." By W. WRIGHT SMITH and H. R. FLETCHER. (See p. 402.)
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JUNE 12, 1947.

Dr. J. W. GREGOR, President, in the Chair.

Mr. ORR read a paper, "Leaf Anatomy of a New Species of *Archeria* from Tasmania," which he illustrated with lantern slides and herbarium specimens. (See p. 472.)

Mr. CAIRD read a paper entitled "Notes on the Occurrence of Apical Vivipary in the Sterile Spikelets of *Cynosurus cristatus* Linn., which he illustrated with lantern slides.

The following papers were read by title:—

1. "Notes on the Scottish Records of *Cuscuta europaea* Linn."
By B. VERDCOURT. (See p. 469.)
 2. "Investigation of the Nature of the 'Push Shoots' of
Galanthus nivalis Linn." By D. KELSALL.
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The Botanical Society of Edinburgh is greatly indebted to the Carnegie Trust for a substantial grant towards the publication of this number of the *Transactions*.